January 2016

The Effects Of Habitat Management On Grassland Birds In The Northern Tallgrass Prairie

Jerry Sterling Cole

THE EFFECTS OF HABITAT MANAGEMENT ON GRASSLAND BIRDS IN THE NORTHERN TALLGRASS PRAIRIE

by

Jerry Sterling Cole, Jr.

Bachelor of Science, Virginia Military Institute, 2012

A Thesis

Submitted to the Graduate Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Master of Science

Grand Forks, North Dakota

May

2016

This thesis, submitted by Jerry Sterling Cole, Jr. in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

_____

Dr. Brett Goodwin

_____

Dr. Kathryn Yurkonis

_____

Dr. Chris Merkord

This thesis is being submitted by the appointed advisory committee as having met all of the requirements of the School of Graduate Studies at the University of North Dakota and is hereby approved.

_____

Wayne Swisher

Dean of the School of Graduate Studies

_____

Date

PERMISSION

Title The effects of habitat management on grassland birds in the northern tallgrass prairie.

Department Biology

Degree Master of Science

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the library of the University shall make it freely available for inspection. I further agree that permission for the extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in his absence, by the Chairperson of the department or the dean of the School of Graduate Studies. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Jerry Sterling Cole, Jr.

May 2016

TABLE OF CONTENTS

LIST OF FIGURES viii

LIST OF TABLES x

ACKNOWLEDGEMENTS xii

ABSTRACT xiiii

CHAPTER

I. REVIEW OF GRASSLAND BIRD VEGETATION ASSOCIATIONS 1

Threats to Grassland Birds 1

Vegetation Effects 2

Management Effects 3

Study Aims 4

Literature Cited 7

II. THE EFFECT OF VEGETATION ON SIX GRASSLAND BIRD SPECIES IN THE NORTHERN PLAINS 11

Abstract 11

Introduction 12

Methods 16

Study Area 16

Site Selection 17

Bird Survey Point Placement 18

Bird Survey 19

Vegetation Survey 20

Vegetation Structure Data Analysis 21

Bird Abundance Analysis 21

Model Selection 23
Detection Model 24
Vegetation Structure Model 25
Final Habitat Model 25
Results 26
Discussion 31
Literature Cited 36
III. THE EFFECT OF LATE SEASON PRESCRIBED BURNING ON GRASSLAND BIRDS IN A REMNANT TALLGRASS PRAIRIE 65
Abstract 65
Introduction 66
Methods 69
Study Area 69
Bird Survey Point Placement 70
Bird Survey 70
Vegetation Survey 71
Vegetation Structure Change Analysis 72
Bird Abundance Analysis 73
Model Selection 75
Detection Model 76
Vegetation Structure Model 76
Final Habitat Model 77
Prescribed Burning Analysis 78
Results 79
Discussion 83
Literature Cited 89
IV. CONCLUSION 112

Literature Cited 115

LIST OF FIGURES

Figure Page

1. Map of sampling locations throughout Grand Forks County, ND 44
2. Diagram illustrating the sampling framework 45
3. Illustration of the 2015 point replacement procedure for any 2014 points falling in a wetland or within 50 m of a wetland 46
4. Boxplots of annual percentage of grass coverage and woody plants per ha at bird points in grazed, hayed, and idle sites 49
5. Boxplots of visual obstruction reading and litter depth in 2014 and 2015 at bird points in grazed, hayed, and idle sites 50
6. Boxplots of percentage bare ground and live vegetation height in 2014 and 2015 at bird points in grazed, hayed, and idle sites 51
7. Predicted Bobolink abundance with 95% confidence intervals 58
8. Predicted Clay-colored Sparrow abundance with 95% confidence intervals 59
9. Predicted Le Conte's Sparrow abundance with 95% confidence intervals for 2015 60
10. Predicted Sedge Wren abundance with 95% confidence intervals 61
11. Predicted Western Meadowlark abundance with 95% confidence intervals 63
12. Standardized predicted bird abundance relative to VOR in 2014, with entire range of measured VOR values displayed 64
13. Standardized predicted bird abundance relative to VOR in 2015, with range of measured VOR values displayed 62
14. Map of Oakville Prairie Field Station sampling locations 96

15. Example of a typical management unit at Oakville 97

16. Mean predicted abundance of Bobolink (A) and Sedge Wren (B) in pre-burn and post-burn seasons 106

17. Mean predicted abundance of Western Meadowlark(A) and Clay-colored Sparrow (B) in pre-burn and post-burn seasons..... 107

18. Mean predicted abundance of Savannah Sparrow in pre-burn and post-burn seasons 108

19. Difference in mean Bobolink abundance between unburned and burned treatments in 2015..... 109

20. Difference in mean Sedge Wren abundance between unburned and burned treatments in 2015..... 110

21. Difference in mean Western Meadowlark abundance between unburned and burned treatments in 2015..... 111

LIST OF TABLES

Table Page

1. Candidate models for the full habitat model selection process....47
2. Candidate models for the vegetation structure model selection process....47
3. Results of a one-way ANOVA with Welch's correction for unequal variance testing effects of management type (hayed, grazed, idle on mean vegetation measures....48
4. Top models for each bird species in each year. 52
5. Estimates of beta coefficients for detection-covariates (p), and abundance covariates (λ) for Bobolink and Clay-colored Sparrow for 2014 and 2015.....53
6. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Le Conte's Sparrow and Savannah Sparrow for 2014 and 2015 54
7. Estimates of beta coefficients for detection-covariates (p), and abundance covariates (λ) for Sedge Wren and Western Meadowlark for 2014 and 2015....55
8. Top models from the vegetation structure model selection process....56
9. Top models from the final habitat model process....57
10. Description of all candidate models for the vegetation structure model selection process....98
11. Description of all candidate models for the final habitat model selection process....98
12. Comparison of change in vegetation structure from 2014 to 2015 in burned and unburned units....99

13. Pearson's correlation coefficients between measures of vegetation structure in 2014 and 2015 99

14. Top models from the detection model selection process 100

15. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Bobolink and Clay-colored Sparrow for 2014 and 2015 101

16. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Savannah Sparrow and Sedge Wren for 2014 and 2015 102

17. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Western Meadowlark for 2014 and 2015 103

18. Top models from the vegetation structure model selection process 104

19. Top models from the final habitat model process 105

20. Log-scale beta coefficient estimates for bird response to burning treatment when accounting for detection probability 105

ACKNOWLEDGEMENTS

I wish to thank my academic advisor Brett Goodwin for providing me the opportunity to attend graduate school and taking a chance on a questionable student. Thanks to the members of my academic committee, Kathryn Yurkonis and Chris Merkord for giving guidance and support for my academic pursuits and my career. I would like to thank Taza Schaming for first introducing me to avian ecology and the joys of fieldwork. Thanks to Asya Rahlin for giving me guidance and encouragement during my graduate career.

I am sincerely appreciative of those who have assisted me in the field with data collection, Bryon Deal, Ann Danielson and Sami Schwartz. My project would not have been possible without access to privately owned lands in North Dakota, thank you to all those who have tolerated me surveying their property during those early summer mornings. A special thanks to the Thorsgard family for so willingly allowing me access to their grazing lands.

This project was made financially possible by a North Dakota State Wildlife Grant awarded by the U.S. Fish and Wildlife Service. Thank you to the North Dakota Department of Game and Fish for allowing me access to their hayed properties and their willingness to discuss grassland management in the region.

ABSTRACT

Grassland birds have been under threat since tallgrass prairie was first used for agricultural cultivation and grassland acreage continues to be converted for row-crop agriculture. The loss of suitable native habitat for grassland birds makes effective management of the little grassland that remains that much more important. While it is widely recognized that grassland birds use vegetation cues for habitat settlement during the breeding season, little study has been done on how vegetation structure influences grassland bird abundances in the northern tallgrass prairie, particularly vegetation structure as it is shaped by different forms of management. Therefore this study aims to determine the most important forms of vegetation structure to breeding grassland birds, and how management actions influence that structure. The effects of grazing, haying, and idle management were examined across 17 sites in 2014, and 16 sites in 2015 in Grand Forks County, ND. I surveyed the bird community during the peak of the grassland bird breeding season. Vegetation structure was measured in early July each year. Measures of vegetation highly overlapped between hayed, grazed, and idle sites, though there was significantly more bare ground and vegetation was less dense in grazed versus hayed and idle sites. I analyzed the six most abundant grassland bird species using N-mixture modeling in package 'unmarked' in program R. For the majority of species, bird abundance was most related to vegetation density and showed no significant effect of percentage of grass, bare ground, and number of woody plants.

However, Clay-colored Sparrow was positively associated with number of woody plants. During the same two seasons the bird community and vegetation structure were monitored at Oakville Prairie Field Station in Grand Forks County, ND. The site had prescribed burning applied during fall 2014, after lacking management for more than 30 years. There was little change in most measures of vegetation after burning, though litter depth and live vegetation height both declined in burned units relative to unburned. Five grassland bird species were examined for vegetation associations using N-mixture modeling and a multi-step modeling procedure. Three of the five species had a significant change in abundance after burning. Bobolink and Sedge Wren abundance declined in burned units, while Western Meadowlark abundance increased. The vegetation measure that best explained Bobolink and Sedge Wren abundance changed from vegetation density in the pre-burn year to litter depth in the post-burn year, suggesting that litter depth may be an important indicator of disturbance for these two species. Overall, these results suggest that a variety of management (e.g. haying, grazing, burning, and idling) could be more beneficial to multiple bird species, by providing a range of vegetation structure from sparse to dense vegetation. Additionally prescribed fire may not have a strong effect on vegetation structure in the first year of burning after a long idle period, though birds may still respond to these small changes in vegetation.

CHAPTER I

REVIEW OF GRASSLAND BIRD VEGETATION ASSOCIATIONS

Threats to Grassland Birds

Grassland birds are among the most imperiled avian group in North America, with population declines of >30% from 1968-2011 (Sauer et al. 2013).The loss of grassland birds has been primarily due to conversion of grassland habitat, with <4% of tallgrass prairie remaining and <0.1% of prairie remaining in areas useful for agricultural cultivation (Samson and Knopf 1994). Additional factors contributing to the decline of grassland bird populations include habitat fragmentation, increasing woody vegetation, and degradation of existing grasslands (Brennan and Kuvelsky 2005). The sensitivity of grassland birds to habitat fragmentation is variable between regions and species, generally larger areas of contiguous grassland have higher bird abundances (Ribic et al. 2009). The relationship between grassland birds and fragmentation appears to be driven by their avoidance of habitat edge, since larger areas of habitat have less edge which often decreases predation risk (Winter et al. 2000). Many grassland bird species have demonstrated an avoidance of woody vegetation, specifically trees (Thompson et al. 2014, Ellison et al. 2013), with one study finding an increase in nesting after removal of tree rows from grassland sites (Ellison et al. 2013). Presumably grassland birds exhibit this avoidance behavior to lower their predation risk, and avoid nest parasitism by other avian species.

Parasitism of bird nests by Brown-headed Cowbirds (*Molothrus ater*) can be strongly influenced by the presence of trees, with nests placed closer to trees having a higher likelihood of being parasitized (Saunders et al. 2003). The value of habitat to grassland birds can be degraded when vegetation is more homogeneous, which can be caused by traditional rotational grazing (Derner et al. 2009) or by leaving grassland idle. Historically prairie was shaped by interactions between grazers like bison (*Bison bison*) and fire, with patches of recently burned grassland preferentially grazed because of a flush of new vegetation (Knapp et al. 1999). One contemporary management of habitat for grassland birds uses the patch-burn grazing paradigm which creates a variety of habitat structure across contiguous area of grassland by burning and grazing rotationally (Fuhlendorf et al. 2001). This is essentially an attempt to artificially replicate the historical disturbance regime. Since grassland bird species preferentially use different types of vegetation structure, having a mosaic of structure on the landscape provides habitat for a larger suite of grassland birds.

Vegetation Effects

Grassland vegetation structure plays a central role in determining how suitable a site is for breeding grassland birds. Preferences range from species to species from tall, dense vegetation to short and sparse vegetation (Wiens 1973). There are a variety of reasons for differential habitat associations among grassland birds, but presumably birds use habitat that balances the risks of nest predation and nest parasitism while providing access to food. The most frequently studied aspect of grassland bird habitat associations may be nest survival relative to vegetation structure (e.g. Davis et al. 2005,

and Winter et al. 2005a, Grant et al. 2006). For instance, Clay-colored Sparrows (*Spizella pallida*) nesting in higher density vegetation had higher nest survival rates, but vegetation density had no significant influence on Savannah Sparrow (*Passercullus sandwichensis*) or Bobolink (*Dolichonyx oryzivorus*) nest survival (Kerns et al. 2010). This suggests that for some bird species, vegetation density exerts little selective pressure for the use of specific vegetation structure, hinting that other forces such as food availability or foraging efficiency may drive the evolutionary link to a particular vegetation structure.

Management Effects

The primary means of generating variation in grassland vegetation in North America is through the use of haying, grazing, patch-burn grazing, and prescribed burning. Each of these forms of management have benefits and drawbacks for grassland birds, with the effects varying among bird species. Haying benefits species that prefer sparser more open habitat like Henslow's Sparrow (*Ammodramus henslowii*), and Grasshopper Sparrow (*Ammodramus savannarum*). Although haying can reduce vegetation density, if a field is hayed while nests are occupied by young, nest failure is assured (Perlut et al. 2006). It has been recommended that haying be restricted to times when the majority of fledglings are capable of escaping haying machinery (Perlut et al. 2006).

Like haying, grazing reduces vegetation density with variable effects on grassland bird species. A study in Kentucky found Grasshopper Sparrows had lower reproductive success in grazed areas versus ungrazed areas presumably due to more

open habitat making nests more visible to predators (Sutter and Ritchison 2005). In a North Dakota study, Grasshopper Sparrows were most abundant at intermediate grazing intensity and lowest in pastures with the lowest grazing intensity, while Marbled Godwits (*Limosa fedoa*) were relatively unaffected by vegetation density (Ahlering and Merkord 2016). Rotational grazing and burning have been used to enhance grassland bird richness by generating a shifting mosaic of undisturbed units with denser, taller vegetation and grazed units with sparser, shorter vegetation (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006).

Prescribed burning affects grassland birds similarly to haying and grazing by reducing the density of vegetation. A study in mixed-grass prairie found declines in grassland bird species richness the year after burning, with richness rebounding two or three years post-burn (Grant et al. 2010). One of the primary differences in vegetation structure between burned and unburned areas is that standing dead vegetation and litter are significantly reduced with burning (Grant et al. 2010). Litter depth has been shown to be a strong predictor of grassland bird abundance, highlighting the possible importance of burning in generating habitat for a range of bird species (Swengel and Swengel 2001).

Study Aims

This study generally aims to determine how vegetation structure, generated by either grazing, haying, or prescribed burning, affects the abundance of six grassland bird species in Grand Forks County, ND. I choose the six most abundant grassland bird species for analysis, since sparse observations of birds could lead to large uncertainty in

abundance estimates (Kéry and Royle 2016). I selected Bobolink, Clay-colored Sparrow, Le Conte's Sparrow (*Ammodramus leconteii*), Savannah Sparrow, Sedge Wren (*Cistothorus platensis*), and Western Meadowlark (*Sturnella neglecta*) for analysis based on their abundances within two sampling seasons.

The aim of Chapter II is to determine which measure of vegetation structure in hayed, grazed, and idle grassland sites across Grand Forks County most strongly affects grassland bird abundance for each of the six species of interest. Gaining a better understanding of habitat associations of grassland birds in the northern tallgrass prairie is particularly important since grassland bird-vegetation associations vary among regions (Bakker 2002). Few studies have examined grassland bird-vegetation associations across multiple management types with most studies sampling on lands managed in a single way. This study aims to describe bird-vegetation associations across a broad range of management types creating a broad range of vegetation structure. These results will be compared to those observed within tallgrass prairie and other grassland ecoregions.

The aim of Chapter III is to determine how the onset of prescribed burning changes vegetation structure on a remnant tallgrass prairie, that has been idle for more than 30 years, and how those changes affect the abundance of grassland birds. Additionally, I aim to determine which measure of vegetation structure bird species respond to both before and after prescribed burning. A better understanding of the vegetation features that birds use to make habitat settlement decisions after

disturbance, will allow managers to focus their efforts on modifying vegetation structure components most important to grassland birds.

Literature Cited

Ahlering, M. A., and C. L. Merkord. 2016. Cattle grazing and grassland birds in the northern tallgrass prairie. Journal of Wildlife Management 80:Early View Online.

Bakker, K., D. Naugle, and K. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds : an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107:605.

Derner, J. D., and A. J. Whitman. 2009. Plant interspaces resulting from contrasting grazing management in northern mixed-grass prairie: implications for ecosystem function. Rangeland Ecology & Management 62:83–88.

Ellison, K., C. Ribic, and D. Sample. 2013. Impacts of tree rows on grassland birds and potential nest predators: a removal experiment. PLoS one 8:e59151.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625.

Fuhlendorf, S., W. Harrell, D. Engle, R. Hamilton, C. Davis, and D. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Grant, T. A., E. M. Madden, T. L. Shaffer, and J. S. Dockens. 2010. Effects of prescribed fire on vegetation and passerine birds in northern mixed-grass prairie. Journal of Wildlife Management 74:1841–1851.

Kerns, C. K., M. R. Ryan, R. K. Murphy, F. R. Thompson, and C. S. Rubin. 2010. Factors affecting songbird nest survival in northern mixed-grass prairie. Journal of Wildlife Management 74:257–264.

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. First edition. Elsevier, London, UK.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications 16:2235–2247.

Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugle, K. K. Bakker, D. W. Sample, and R. B. Renfrew. 2009. Area sensitivity in North American grassland birds: patterns and processes. Auk 126:233–244.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Sauer, J., W. Link, and J. Fallon. 2013. The North American breeding bird survey 1966-2011: summary analysis and species accounts. North American Fauna 79:1–32.

Saunders, C. A., P. Arcese, and K. D. O'Conner. 2003. Nest site characteristics in the song sparrow and parasitism by brown-headed cowbirds. Wilson Bulletin 115:24–28.

Sutter, B., and G. Ritchison. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of grasshopper sparrows. Journal of Field Ornithology 76:345–351.

Swengel, S. R., and A. B. Swengel. 2001. Relative effects of litter and management on grassland bird abundance in Missouri, USA. Bird Conservation International 11:113–128.

Thompson, S. J., T. W. Arnold, and C. L. Amundson. 2014. A multiscale assessment of tree avoidance by prairie birds. Condor 116:303–315.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

.

CHAPTER II

THE EFFECT OF VEGETATION ON SIX GRASSLAND BIRD SPECIES IN THE NORTHERN PLAINS

Abstract

Grassland birds have declined throughout North America since they have been monitored, therefore understanding how to improve grassland habitat that remains is particularly important for these species. Much work has been done to determine grassland bird species vegetation preferences which can vary between regions and seasons. Few studies have examined the vegetation preferences of grassland birds across a broad spectrum of management regimes, making generalizations from studies that focus on single management practice difficult. The objective of this study was to examine how birds respond to vegetation structure across hayed, grazed, and idle sites in northern tallgrass prairie. I surveyed the avian and vegetation community at 17 grassland sites in 2014 and 16 grassland sites 2015 in Grand Forks County, North Dakota, during the grassland bird breeding season. Vegetation structure was highly variable among similarly managed sites. In 2014, there was no detectable difference in vegetation structure among sites under different management. In 2015, grazed sites had lower vegetation density, litter depth, and more bare ground than hayed and idle sites. I evaluated the relationship between bird abundance and vegetation using binomial N-mixture modeling. Top models explaining bird abundance included vegetation density for three of six species in 2014, and five of six species in 2015.

Woody vegetation did not affect four of six species. Only Clay-colored Sparrow showed a consistent positive association with woody vegetation. My results suggest that in the northern tallgrass prairie, vegetation density may be the most important characteristic of vegetation structure for grassland birds and by having a variety of management on the landscape a full suite of grassland birds may be better supported.

Introduction

Grassland birds have shown the most dramatic decline of any avian group in North America (Peterjohn and Sauer 1999). This rapid loss has been linked to habitat reduction, increasing woody vegetation, habitat fragmentation, and increasing vegetation homogeneity at landscape and site scales (Brennan and Kuvlesky 2005). While landscape conditions such as grassland patch size (Winter et al. 2006) and landscape habitat composition (Cunningham and Johnson 2006) affect birds, understanding characteristics surrounding their site use are most important for site management decisions. Given the strong variation in bird nesting and feeding ecology that exists among grassland birds, it is not surprising that the most well examined aspect of grassland bird ecology is how species associate with specific vegetation characteristics (Wiens 1969, Wiens 1973, Wiens 1974, Davis 2004, Winter et al. 2005a, Augustine et al. 2015). Vegetation characteristics not only affect habitat use (Hovick et al. 2015), but can also affect demographic rates such as nest survival (Winter et al. 2006). With a more detailed understanding of grassland bird vegetation preferences, habitat can be more strategically managed to meet population management goals.

Grassland birds have adapted to occupy varying physical niches within heterogeneous grasslands (Wiens 1969) and are known for their wide variation in habitat preferences. For example, Bobolinks (*Dolichonyx oryzivorus*) are more abundant in moderately dense vegetation, while Savannah Sparrows (*Passerculus sandwichensis*) are associated with sparser, shorter vegetation (Thompson et al. 2014). This wide range of habitat preferences amongst species presumably arose in response to structural heterogeneity that was once generated through the interaction of periodic burning and bison (*Bison bison*) grazing within North American grasslands. Bison preferentially graze recently burned areas over areas with one or two growing seasons since burning. As a result after an initial burn followed by brief, intense grazing, vegetation density and litter depth increase over time (Fuhlendorf et al. 2008). This interaction of burn history and grazing results in the development of landscape scale heterogeneity in vegetation structure to which birds respond (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Hovick et al. 2014). Unfortunately, the cessation of fire and grazing activity within the last hundred years has removed these natural processes maintaining landscape heterogeneity, and, as a result, grasslands have become much more homogenous both within and across sites (Knapp et al. 1999).

Recent efforts to enhance vegetation structural heterogeneity through grassland management have had mixed results. Even with the history of variation in vegetation structure in grasslands, bird species have shown both negative and positive responses to increased structural heterogeneity at small scales (i.e. survey unit level; Wiens 1974). However, when vegetation structure varies across sites within a landscape, individual

species abundances and overall bird richness increase (Fuhlendorf et al. 2006, Hovick et al. 2014). Currently, grassland vegetation heterogeneity is generated by application of prescribed burning and grazing (Fuhlendorf and Engle 2001, Hovick et al. 2015, Alhering and Merkord 2016). Hovick et al. (2015) found that all the grassland bird species considered in their study increased in abundance with time since burning and grazing, and four of five species increased with increasing landscape structural heterogeneity. The fact that grassland bird richness increases with landscape heterogeneity (Fuhlendorf et al. 2006) is not surprising given that grassland bird species have specific vegetation preferences. Clay-colored Sparrow (*Spizella pallida*) prefers shrubby areas (Winter et al. 2004) and Grasshopper Sparrows (*Ammodramus savannarum*) are negatively associated with shrubs (Ahlering et al. 2009), while Le Conte's Sparrow (*Ammodramus leconteii*) prefers denser vegetation (Winter et al. 2005b).

It is important to understand avian responses along the entire vegetation gradient generated by management actions, since most grassland bird studies have focused on bird responses to specific management without considering what characteristics of vegetation contribute to the response. Furthermore, few studies have examined grassland bird vegetation associations across sites that vary in their management (e.g., Danley et al. 2004, McMaster et al. 2005, Sutter and Ritchison 2005, but see Swengel and Swengel 2001). Studies of the vegetation associations of grassland birds in North Dakota have primarily been conducted in large contiguous areas of grassland, such as the Sheyenne National Grassland in southeastern part of the state

(e.g., Winter et al. 2005a, Cunningham and Johnson 2006, Ahlering and Merkord 2016) or in mixed-grass prairie in western North Dakota (e.g., Madden et al. 2000). It important to determine bird-vegetation associations in a variety of habitat configurations and regions, like northeastern North Dakota that has grassland fragments interspersed with fields used for row crop agriculture. It is risky to make generalizations from other regions about the vegetation associations of bird species, since regional differences in climate conditions could shift associations.

I surveyed grassland bird and vegetation structure over two seasons on hayed, grazed, and idle grasslands to maximize the variety of vegetation structure and composition, so the results could be applied more broadly. The primary objective for this study was to describe the vegetation components that best explained grassland bird abundance in northeastern North Dakota. Knowing the vegetation associations for three of six of the study species, Bobolink, Le Conte's Sparrow, and Western Meadowlark (*Sturnella neglecta*), is particularly important because they are Species of Conservation Priority (SoCP) in North Dakota. These birds have been designated by North Dakota Game and Fish as high priority due to their declining status, or their relative high abundance in North Dakota compared to other regions suggesting the importance of habitat in the state (Dyke et al. 2015). Although the three remaining species, Savannah Sparrow, Sedge Wren (*Cistothorus platensis*), and Clay-colored Sparrow, are not SoCP it is important to understand the preferences of these more common species so we can continue to maintain their relatively large populations (Berlanga et al. 2010). By knowing habitat associations for grassland birds in this

region, remaining grassland patches can be more strategically managed to benefit a full suite of grassland birds.

Methods

Study Area

This study took place within the Grand Forks County Prairie Project area in northeastern North Dakota (Figure 1), (Centroid: 47.92191 °W, -97.45693 °N). The region is comprised of large patches (~260 ha) of hayed, grazed, idle, burned, and unmanaged grassland within a larger row-crop agricultural matrix. The study area is situated within the northern tallgrass prairie ecoregion (Omernik and Gallant 1987). The majority of sites are dominated by Smooth brome (*Bromus inermis*), Western wheatgrass (*Pascopyrum smithii*), Kentucky bluegrass (*Poas praetensis*), and yellow sweet clover (*Melilotus officinalis*). The dominant woody species are Western snowberry (*Symphoricarpos occidentalis*), prairie rose (*Rosa arkansana*), and Russian olive (*Elaeagnus angustifolia*). In 2014 annual precipitation was 55.91 cm and mean temperature of 8.8°C, ranging from -16.8°C in January, to 19.9°C in August (National Oceanic and Atmospheric Administration [NOAA] 2014). Annual weather summaries are not yet compiled for 2015. During the peak grassland bird breeding period, May-July, the mean of average monthly air temperature was 16.90 °C ± 2.24 SE for 2014 (NOAA 2014) and 17.70 °C ± 2.85 SE for 2015 (NOAA 2015). For the same period the mean of monthly accumulated precipitation was 10.74 mm ± 3.27 SE in 2014 and 9.82 mm ± 2.03 SE in 2015, and in 2014 accumulated precipitation was highest in June

(17.14 mm) and lowest in May (6.35 mm), and in 2015 precipitation highest in July (12.57 mm) and lowest in June (5.86 mm).

Site Selection

Grassland sites within the study area that were hayed, grazed, or idle during the study seasons were selected. Potential sites were identified by visually inspecting the 2013 National Agricultural Statistic Service (NASS) cropland data layer and 2013 National Agriculture Imagery Program (NAIP) aerial imagery. Landowners with North Dakota or Minnesota addresses within the Grand Forks County GIS parcel database (http://gfgis1.nd.gov/gfcimsv2) were solicited for property access by mail, as these were deemed most likely to respond to request for access. Additionally, public lands within our study area were also included as potential sampling sites.

Sites were preferentially selected if they were in close proximity to a drivable road, and spaced at least 1 km apart. Due to limited availability of hayed sites in our study area, we sampled Wildlife Management Areas (WMAs) managed by the North Dakota Game and Fish Department (n=2). These sites were mowed annually in late-July. Grazed sites (2014: n=4, 2015: n=5) were actively grazed during the survey seasons and I observed stocking densities ranging from 0.2-0.6 head/ha. Idle sites (2014: n=11, 2015: n=9) were not actively managed with haying, grazing, or burning and were all enrolled in the Conservation Reserve Program (CRP) administered by the Natural Resources Conservation Service (NRCS). I surveyed 17 sites in 2014 from June 3-July 5 and 16 sites in 2015 (4 sites were replaced from 2014) from May 28-June 29.

Bird Survey Point Placement

In sites with square configurations (2014: n=14, 2015: n=13), I placed five bird survey points, hereafter bird points. Initially, a bird point was placed at the centroid (geometric center) of each site and four additional bird points were placed in the NW, NE, SE, and SW regions of each site at a random distance ≥ 225 m from the central bird point and ≥ 150 m from borders (Figure 2) using ArcGIS 10.1 (ESRI, Redlands, California, USA). In sites with alternative configurations (2014: n=3, 2015: n=3) a bird point was placed at the centroid of each site, buffers applied as described above and 1 to 4 additional points placed randomly within the remaining site area depending on site area.

Several initial bird points were located in, or near, cattail marshes, a habitat typically excluded from surveys focusing on grassland birds (Madden et al. 2000). These points were sampled in during the first season (2014) and the placement of these points were adjusted for the second survey season (2015). Cattail marsh within each site was hand digitized from 2014 NAIP aerial imagery and 50 m buffers placed around site cattail marsh polygons using ArcGIS 10.1(ESRI, Redlands, California, USA). The 50 m buffer allowed for a balance between sufficient sampling per site, while minimizing the possible negative bias of lower amount of suitable grassland bird habitat. First season bird points falling within either cattail marsh or the 50 m buffer were replaced (n=11) with points placed randomly within the same region (Figure 3) while adhering to the initial placement rules. Bird points were removed (n=5) if no area was available to place a new point nearby.

Bird Survey

I surveyed ~3 sites per morning, starting at local sunrise (~0530), as defined by the U.S. Naval Observatory for Grand Forks, ND, and continuing until 1000. No locations were surveyed during high wind (>4 Beaufort scale), rain, or heavy fog (Winter et al. 2006). Bird points were visited 3 times with surveys ~9 days apart in 2014 and 4 times with surveys ~10 days apart in 2015. The season's weather conditions dictated the maximum number of visits possible to each survey point. The site visit order was alternated to ensure an early (~0530-0700), mid (0700-0830), and late (0830-1000) morning visit for each location.

Upon arrival at each bird point I observed a two-minute rest period (cool-down) to allow birds to return to their positions prior to my arrival. During cool-down, I recorded wind speed, estimated by using the Beaufort scale, time of day, and day of the season. These data were later used as potential detection covariates, variables that could influence the chance of observing a bird species during an individual visit. Immediately following cool-down, all birds were recorded for 5-min, noting all birds seen or heard within a 100 m radius (Bibby et al. 2000). Birds were only counted if they used the habitat in the detection radius, meaning those on the ground or perched on vegetation. Any birds flying over the detection radius were recorded as a flyover and were excluded from analysis. Points within a site were visited consecutively. The counts of visual detections of males, or males and females for species that are not sexually dimorphic, and singing birds were summed and used as abundance measures for each species.

Vegetation Survey

Because vegetation measurements from later in the breeding season have been found to be better predictors of bird abundance than measurements taken earlier in the season (Winter and Faaborg 1999), local vegetation structure and composition was measured at the end of each breeding season. Five vegetation survey quadrats (0.5 × 1.0 m) were sampled within each detection radius. The first quadrat was placed in the center of each radius and four additional quadrats were randomly placed 15-100 m from the central point (Figure 2) using ArcGIS 10.1 (ESRI, Redlands, California, USA). In 2015, five new vegetation quadrats were randomly placed 15-50 m of all bird points using the same methodology as 2014 (Figure 2).

In 2014, overlapping aerial percent cover was estimated to the nearest 5% for every species of plant within each quadrat. Plant species cover values were summed across plant functional groups (forb, grass, and woody) for analysis. In 2015 non-overlapping cover was estimated to the nearest 5% for forbs, grasses (graminoids), and woody plant species. Bare ground coverage was estimated to the nearest 5%. Visual obstruction was measured in 2.5 cm increments in the center of each quadrat from a distance of 4 m and a height of 1.5 m, in each cardinal direction using a Robel pole (Robel et al. 1970). Vegetation height (nearest 0.1 cm) and litter depth (nearest 0.1 cm) measurements followed those outlined by Winter et al. (2004). Vegetation measurements were averaged across the five quadrats to describe the vegetation structure and composition for each bird point. The measure of variation in vegetation structure was the SD of all vegetation quadrat means for each bird point. Both the mean

and SD of vegetation structure were used as vegetation covariates, measures of vegetation that are believed to influence bird abundance, in the following model selection process. The number of shrubs (< 1 m tall) and trees (> 1 m tall) within the detection radius of each bird point were recorded and summed to give an estimate of woody vegetation.

Vegetation Structure Data Analysis

To test if vegetation structure differed between bird points in hayed, grazed and idle management in 2014 and 2015 I used a one-way ANOVA with Welch's correction for unequal variance between groups. To determine which management types were significantly different I followed up any significant ANOVA result ($p<0.05$) with a pairwise t-test with Holm's correction.

Bird Abundance Analysis

The bird abundance analysis was restricted to the six most abundant grassland bird species (>60 detections) observed within each year, since sparse observations of birds could lead to large uncertainty in abundance estimates (Kéry and Royle 2016). I analyzed six grassland bird species: Bobolink, Le Conte's Sparrow, Western Meadowlark, Clay-colored Sparrow, Savannah Sparrow, and Sedge Wren. Le Conte's Sparrow abundance was not modeled in 2014, due to low number of detections (36). Only bird points that were surveyed three times in 2014 (n=39), and four times in 2015 (n=56) were used for analyses, since missing observations may bias estimation of model parameters (Rubin 1976).

The *N*-mixture modeling framework (Royle et al. 2004) in program R (R Core Team 2014) with package 'unmarked' and function 'pcount' (Fiske and Chandler 2011) was used to determine the relationship between bird abundance and vegetation structure. This form of analysis simultaneously considers the effect of covariates (e.g. time of day) associated with the probability of detecting birds and vegetation covariates (e.g. litter depth) associated with bird abundance at a site (Royle et al. 2004). It is important to incorporate detection probability when modeling abundance because most bird species are not detected at the same rate throughout a season or time of day (Rollfinke and Yahner 1990). Without incorporating detection probability, counts could be biased depending on the sampling period. Once detection probability was accounted for, the effect of vegetation covariates was modeled. The aim of using *N*-mixture modeling was to determine which vegetation measures have the greatest effect on bird abundance, when accounting for all sources of variation (i.e., vegetation structure and imperfect detection of individuals).

A requirement of the *N*-mixture model is a closed population, meaning no immigration or emigration during the entirety of the survey period (Royle et al. 2004). This can be reasonably assumed since surveys were conducted during the peak of the grassland bird breeding season, when birds are relatively stationary because they are defending established territories. It has been suggested that violation of closure will be apparent in lack of model fit (Thompson et al. 2014), when tested by parametric bootstrapping in 'unmarked' (Royle et al. 2004). Parametric bootstrapping simulates new bird abundance data by using the estimated parameters of the model. The model's

goodness-of-fit (GOF) was tested by comparing the chi-squared statistic of the real data to the distribution of the chi-squared statistics generated from multiple runs of simulated data through the model (Kéry and Royle 2016).The data from the two years were analyzed separately, since vegetation survey methods differed slightly between years.

Model Selection

A multi-step selection process similar to that employed by Thompson et al. (2014) was used to determine the best model for both detection and vegetation covariates. This process involved three model selection steps. The first step determined which covariates (e.g. time of day) best described detection probability for each bird species. This was done prior to selection of the vegetation covariates because considering the effects of vegetation on bird abundance without accounting for detection could result in false conclusions. The second step was to determine whether one of six typically correlated measures of vegetation structure, VOR, live vegetation height, litter depth, and the SD of those, explained species abundances better than the best detection model. The third step was to determine whether three additional vegetation measures, bare ground, percent of grass, count of woody plants, could be used to further describe bird abundances. This third and final model was then reduced to the most parsimonious model of bird abundance relative to potential detection and vegetation covariates.

For all model selection steps I used Akaike's Information Criterion (AIC) to select the top model (Burnham and Anderson 2002). I did not use AIC corrected for small sample size because it is still unclear what the effective sample size is for *N*-mixture modeling (Kéry and Royle 2016). If the top model was not separated from other competing models by >2 AIC units, I chose the model with the lowest number of covariates and lowest AIC. Both detection and vegetation covariates were standardized by subtracting each covariate value from the group mean, then dividing by the group standard deviation, to maximize model convergence and simplify interpretation (Zuur et al. 2009).

Detection Model

Hours after sunrise, day of the season, and wind speed were included as possible detection covariates. All additive combinations of these covariates were considered during model selection (e.g., time+date+wind, time+wind, time+date…). Interactions were not considered due to my limited sample size. All candidate detection models included the same four vegetation covariates on abundance (VOR, bare ground, number of woody plants, and percent grass coverage) because comparing models with detection covariates but no abundance covariates could result in spurious conclusions (Thompson et al. 2014). Candidate detection models were fitted with a Poisson mixture.

.

Vegetation Structure Model

After selection of detection covariates, I created 14 models to assess the influence of local vegetation structure and structural variation on bird abundance (Table 1). I included mean and SD of VOR, litter depth, and vegetation height for each bird point to test if mean vegetation structure or variation in structure influenced bird abundance. Each model only included a single type of vegetation measure. Quadratic and linear terms were included, since plots of raw abundance showed intermediate peaks. Quadratic terms were not included without the corresponding linear term. The vegetation covariate from the most parsimonious vegetation structure model was included in the final habitat model. For the 2014 models, cattail marsh area (m^2) within 100 m of the bird point was initially included at this stage, since differing amounts of upland grassland habitat may affect bird abundance. If the coefficient for cattail marsh plus standard error overlapped zero it was excluded, and candidate vegetation models reanalyzed.

Final Habitat Model

The final habitat model (FHM) selection combined the top detection covariates and the top vegetation structure covariates selected in the previous steps, with three additional measures of vegetation. I included percent grass coverage, percent bare ground, and number of woody plants. These measures were included in 10 models (Table 2) based on prior knowledge of vegetation characteristics that are important to grassland birds (Fisher and Davis 2010, Thompson et al. 2014). The top

model was selected using AIC rank. If the null or detection only model was included in the list of top models, no vegetation covariates were considered to be reasonable predictors of abundance. I assessed the goodness-of-fit of the most parsimonious FHM for each species by comparing the Pearson's chi-square statistic of the observed data to a distribution of chi-square statistics generated by parametric bootstrapping (MacKenzie and Bailey 2004). A model was considered to have adequate fit if the p-value from the chi-square statistic for observed data when compared to the simulated data was >0.05. I simulated 1000 datasets to test GOF using the Nmix.gof.test function from the 'AICcmodavg' package (Mazerolle 2016). In the interest of clarity I averaged the beta coefficients for bird species that had multiple top models using the package 'AICcmodavg' (Mazerolle 2016).

I used the best FHM for each species to generate predictions of abundance across the entire range of observed vegetation values present in the model. When the best model contained multiple covariates all other terms were held at their mean values while the term of interest was allowed to vary across the range of measured covariate values.

Results

In 2014, management affected the number of woody plants and grass coverage (Table 3), unfortunately, pairwise t-tests could not detect differences between management types (Figure 4). In 2015, management affected VOR, number of woody plants, and bare ground coverage (Table 3). Grazed sites had lower VOR and more bare

ground than hayed or idle sites (Figure 5 and 6). Additionally, grazed sites had fewer woody plants than idle sites (Figure 4).

In 2014 the most frequently detected grassland birds were Savannah Sparrow (24% of all bird detections, 581 total detections), Bobolink (12%, 303), Western Meadowlark (9%, 212), Clay-colored Sparrow (7%, 162), and Sedge Wren (7%, 158). In 2015 the most frequently detected grassland bird were Savannah Sparrow (37% of all bird detections, 838 total detections), Bobolink (10%, 230), Sedge Wren (9%, 213), Western Meadowlark (9%, 210), Clay-colored Sparrow (7%, 154), and Le Conte's Sparrow (3%, 68). Savannah Sparrows were detected at least once at all points surveyed during both years. Savannah Sparrow abundances ranged from 0-7 in 2014 and 0-5 in 2015. The most frequently observed Savannah Sparrow abundance was 3 in 2014 and 4 in 2015. Bobolink were detected at least once at 89% of points in 2014 and 81% in 2015. Bobolink abundances ranged from 0-6 in 2014 and 0-4 in 2015. The most frequently observed abundance for Bobolink was 0 in both years. Western Meadowlarks were detected at least once at 82% of points in 2014 and 70% of points in 2015. Western Meadowlark abundance ranged from 0-5 in 2014 and 0-4 in 2015. The most frequently observed abundance for Western Meadowlark was 0 in both years. Clay-colored Sparrow were detected at least once at 76% of points in 2014 and 66% of points in 2015. Clay-colored Sparrow abundance ranged from 0-6 in 2014 and 0-3 in 2015. The most frequently observed abundance for Clay-colored Sparrow was 0 in both years. Sedge Wren were detected at least once at 68% of points in 2014 and 63% of points in 2015. Sedge Wren abundance ranged from 0-4 in 2014 and 0-4 in 2015. The

most frequently observed abundance for Sedge Wren was 0 in both years. Le Conte's Sparrows were detected at least once at 50% of points in 2015. Sedge Wren abundance ranged from 0-2 in 2015. The most frequently observed abundance for Sedge Wren was 0 in 2015.

Detection probability declined with time of day and increasing wind speed, and increased with day of season for all bird species with the exception of Bobolink which had detection probability consistently decline with day of season. All species abundances were explained by at least one detection covariate over the two-year sampling period (Table 4). In both years, the probability of detecting Bobolinks declined as the season progressed (Table 5). In 2014 the probability of detecting Clay-colored Sparrows increased as the season progressed (Table 5). In 2015 Clay-colored Sparrow detection probability declined as wind speed increased (Table 4). In 2015 Le Conte's Sparrow detection probability declined with time of day (Table 6). In 2014 no covariates sufficiently explained Savannah Sparrow detection. In 2015 Savannah Sparrow detection increased over the season (Table 6). In 2014 Sedge Wren detection probability declined with time of day and increased with day of season (Table 7). In 2015 Sedge Wren detection probability declined with increasing wind speed (Table 7). In 2014 Western Meadowlark detection probability was not adequately explained by any covariates (Table 4). In 2015 Western Meadowlark detection probability declined with time of day (Table 7).

The most parsimonious vegetation structure models included VOR for four of five species in 2014 and four of six species in 2015 (Table 8). Litter depth was not

present in competitive models (ΔAIC<2) in 2014 and was present for two species in 2015. Only in 2015 were measures of vegetation variability competitive as top models, though none were chosen as most parsimonious (Table 8). Bobolink was non-linearly related to VOR in both years. Clay-colored Sparrow was non-linearly related to live vegetation height in 2014 and linearly related to VOR in 2015. Le Conte's Sparrow was non-linearly related to VOR in 2015. Savannah Sparrow was linearly related to VOR in 2014 and no measure of vegetation density in 2015. Sedge Wren was non-linearly related to live vegetation height in 2014 and VOR in 2015. Western Meadowlark was non-linearly related to VOR in both years.

Full FHMs for each of the five species showed adequate fit after testing goodness-of-fit using parametric bootstrapping for Bobolink (2014: p=0.194, ĉ=1.12; 2015: p=0.232 ĉ=1.08), Clay-colored Sparrow (2014: p=0.780, ĉ=0.89; 2015: p=1.000, ĉ=0.68), Le Conte's Sparrow (2015: p=0.720, ĉ=0.89), Savannah Sparrow (2014: p=0.640, ĉ=0.996; 2015: p=1.000, ĉ=0.28), Sedge Wren (2014: p=0.294, ĉ=1.07; 2015: p=0.840, ĉ=0.81), and Western Meadowlark (2014: p=0.474, ĉ=1.00, 2015: p=0.988, ĉ=0.76). Although some species showed signs of underdispersion (ĉ<1.0), a sign of lower variation in bird abundance than would be expected, this can be ignored at the risk of overinflating error (Kéry and Royle 2016). When data is underdispersed error bars around abundance estimates may be larger than is actually correct, making detection of a significant effect more difficult.

Competitive final habitat models in both years, those within 2 ΔAIC units of the top model, included the measure of vegetation selected during the vegetation structure

model process, except for Savannah Sparrow in 2015 (Table 9). The majority of FHMs had either VOR or live vegetation height included in top models (Table 9). VOR^2 was the only vegetation covariate included in the top Bobolink FHMs in both years (Table 9). In 2014 Bobolink abundance peaked at intermediate VOR (29 cm) and in 2015 peaked at denser VOR (46 cm) (Figure 7, Table 5). In 2014 the top FHMs for Clay-colored Sparrow included live vegetation height and number of woody plants, and all vegetation covariates in 2015 (Table 9). In both years Clay-colored Sparrow abundance increased with greater numbers of woody plants (Figure 8). In 2014 model averaged beta-coefficients for Clay-colored Sparrow showed no significant influence of any vegetation measure other than number of woody plants, and in 2015 woody plants and grass coverage significantly affected abundance (Table 6). In 2015 top FHMs for Le Conte's Sparrow all included VOR, with increased bird abundance in denser VOR (Figure 9). In 2014 top FHMs for Savannah Sparrow all included VOR^2 (Table 9), though abundance was significantly affected by VOR, the effect was relatively small (β=-0.15, SE=0.06). In both years Sedge Wren abundance peaked in taller denser vegetation (Figure 10). Model averaged beta-coefficients for Sedge Wren showed no significant influence of any measure of vegetation other than either vegetation height in 2014 or VOR in 2015 (Table 7). In both years top FHMs for Western Meadowlark included VOR (Table 9), with the highest bird abundance in short sparse vegetation (Figure 11). While peaks of bird abundance varied from season to season, there were clear associations of bird species with vegetation structure generated by different management types (Figures 12 and 13). Savannah Sparrow and Western Meadowlark were generally associated with

sparse vegetation density typical of grazed management, Bobolink with intermediate to dense vegetation, and Le Conte's Sparrow, Sedge Wren and Clay Colored Sparrow with dense vegetation (Figures 12 and 13).

Discussion

The most consistent predictor of grassland bird abundance was VOR, suggesting that the most effective management actions may be those that affect vegetation density. Sampling grasslands with a variety of management allowed for assessment of bird responses along a greater gradient of vegetation structure than would be possible by sampling one management type. This allowed me to assess non-linear responses to vegetation variables. Previous studies that limited sampling to a single type of management found mostly linear relationships with vegetation structure (Madden et al. 2000, Thompson et al. 2014). Surprisingly, in my study bird abundances were not affected by bare ground, grass cover, and number of woody plant species, even though previous studies have linked these vegetation measures with grassland birds (e.g. Fisher and Davis 2010, Thompson et al. 2014). There was considerable variation in vegetation preferences among bird species and between years. Since almost all breeding grassland birds are migratory, wide swings in densities between years could be unrelated to differences in local breeding habitat (Rushing et al. 2016). This further emphasizes the importance of long-term studies given the variability inherent in this system.

The grassland bird associations with vegetation height and density I observed were mostly consistent with previous literature. Bobolink, Sedge Wren, and Le Conte's Sparrow abundances peaked at mid and high vegetation densities. In previous studies Bobolink abundance increased with vegetation height, but showed no support for a quadratic relationship (Winter et al. 2005a, Thompson et al. 2014), possibly due to restricting sampling to one management type. Le Conte's Sparrow (Madden et al. 2000, Hovick et al. 2014) and Sedge Wren (Thompson et al. 2014) have also shown preferences for denser vegetation. Consistent with my results, Western Meadowlarks were previously associated with relatively sparse vegetation in eastern North Dakota (Madden et al. 2000), but were associated with intermediate density vegetation in the southern tallgrass prairie (Hovick et al. 2014). The differences in association could be due to the relative nature of density of vegetation in these two regions. Savannah Sparrow's preference for shorter vegetation (Thompson et al. 2014, Madden et al. 2000), was confirmed by my results. Consistent with previous literature (Thompson et al. 2014) Clay-colored Sparrows were not significantly affected by vegetation density, presumably because woody vegetation is more important for habitat use. Clay-colored Sparrows closer association with woody vegetation instead of vegetation density is logical, given that this species has higher nest survival when nests are located in relatively dense shrub habitat (Grant et al. 2006).

The variation in bird vegetation associations between years could be due to seasonal fluctuations in precipitation and temperature. Since precipitation and temperature are closely tied to grassland productivity in the Great Plains (Epstein et al.

1997), birds are likely responding to changes in vegetation structure generated by seasonal conditions. Although there was little difference in the mean temperature and precipitation during the two survey seasons, the timing of precipitation was different, which could have altered available vegetation structure. Other studies of grassland birds have found strong relationships between change in precipitation and bird productivity (George et al. 1992), changes in bird abundance (Niemuth et al. 2008), and grassland bird associations with vegetation structure (Ahlering and Merkord 2016).

Though many have found a negative relationship between increased woody plant abundance and grassland birds (e.g. Madden et al. 2000, Davis et al. 2004, Cunningham and Johnson 2006, Thompson et al. 2014), the majority of top models in this study showed only a weak negative relationship with woody vegetation when a measure of vegetation height or density was included in the model. Additionally the number of woody plants was not present alone in top models, suggesting that it may play a limited role in habitat selection at my study sites. Although bird species in our study may lack sensitivity to woody vegetation, it is more likely that the range of woody vegetation present across all sites may have been too little to elicit a response if grassland birds have a threshold number of woody plants at which they actively begin avoiding areas.

By continuing to assess grassland bird habitat associations in other regions, we can further refine our understanding vegetation preferences that may differ due to regional differences like climate, soil type, and community composition. Without a thorough assessment of grassland bird-vegetation associations, managers may be

creating habitat that is mismatched to the adaptations of birds for their region. In the northeastern region of North Dakota, a large portion of existing grassland is maintained under the Conservation Reserve Program (CRP), which is usually characterized by dense vegetation since some sites are typically managed only once during the lifetime of the CRP contract. This management is termed mid-contract management (MCM), and can be enacted through either disking, burning, herbicides, or inter-seeding. Due to lack of disturbance and seeding mixture CRP is typically tall dense grass (Vickery et al. 2007), and only a portion of the grassland bird community like Le Conte's Sparrows and Sedge Wrens that preferentially use these areas are present in relatively high densities. If habitat like CRP is continued to be left idle across the landscape, the grassland bird community may shift to being dominated by species that preferentially select dense habitat and species that are associated with sparse or intermediate vegetation forced to adapt to available conditions, with concomitant decreases in population size.

To maintain grassland bird richness on the landscape, a mosaic of managed lands have to be maintained, rather than a patchwork of grassland that has relatively homogeneous vegetation (Fuhlendorf et al. 2006). While patch level management is typically implemented on large swaths of publicly owned land, it may be helpful to work with landowners enrolled in CRP to encourage a coordinated management regime by rotating management on parts of the landscape that have large amounts of contiguous grassland. For instance, owners of a full section of grassland could each hay their ¼ section on a 4 year rotation, so there is a mosaic of vegetation structure on the landscape. Though some authors have suggested that larger units of patch-burned

pasture are better for grassland bird richness (Hovick et al. 2015), there has been no study that has determined optimal size for disturbed patches. It is still unclear at what size discrete patches should be created to maximize avian richness, this has been left untested presumably because large scale manipulation of grassland is logistically and financially difficult. Maintaining grassland birds on the landscape will continue to require a balance of cooperation between private and public partners, since lands enrolled in CRP are typically left idle and could support a more diverse bird community if a mixture of management was implemented on a portion of this land.

Literature Cited

Ahlering, M. A., D. H. Johnson, and J. Faaborg. 2009. Factors associated with arrival densities of grasshopper sparrow (Ammodramus savannarum) and baird's sparrow (A. bairdii) in the Upper Great Plains. Auk 126:799–808.

Ahlering, M. A., and C. L. Merkord. 2016. Cattle grazing and grassland birds in the northern tallgrass prairie. Journal of Wildlife Management 80:Early View Online.

Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. Vickery. 2007. Conservation of grassland birds in North America : understanding ecological processes in different regions. Ornithological Monographs 64:1–46.

Augustine, D. J., and J. D. Derner. 2015. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. Journal of Wildlife Management 79:927–936.

Bakker, K., D. Naugle, and K. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Berlanga, H., J. A. Kennedy, T. D. Rich, M. C. Arizmendi, C. J. Beardmore, P. J. Blancher, G. S. Butcher, A. R. Couturier, A. A. Dayer, D. W. Demarest, W. E. Easton, M. E. Gustafson, E. A. Iñigo-Elias, A. O. Krebs, V. Panjabi, R. Contreras, K. V. Rosenberg, J. M. Ruth, E. S. Castellón, R. M. Vidal, and T. Will. 2010. Saving our shared birds: partners in flight tri-national vision for landbird conservation project. Partners in Flight. Ithaca, NY.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird census techniques. Second Edition. Academic Press, London, UK.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds : an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media. New York, USA.

Coppedge, B. R., S. D. Fuhlendorf, W. C. Harrell, and D. M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. Biological Conservation 141:1196–1203.

Cunningham, M., and D. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062–1075.

Danley, R. 2004. Species diversity and habitat of grassland passerines during grazing of a prescribed-burned, mixed-grass prairie. Western North American Naturalist 64:72–77.

Davis, S. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121:1130–1145.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12:53–64.

Dyke, S. R., S. K. Johnson, and P. T. Isakson. 2015. North Dakota State Wildlife Action Plan. North Dakota Game and Fish Department. Bismarck, ND.

Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1997. Productivity patterns of C3 and C4 functional types in the U.S. Great Plains. Ecology 78:722–731.

Fisher, R., and S. Davis. 2010. From Wiens to Robel: a review of grassland bird habitat selection. Journal of Wildlife Management 74:265–273.

Fiske, I., and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Applied Ecology 41:604–614.

Fuhlendorf, S., W. Harrell, D. Engle, R. Hamilton, C. Davis, and D. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Grant, T. A., E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmas. 2006. Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70:691–701.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5:1-13.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications 25:662–672.

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. Applied Hierarchical Modeling in Ecology. First edition. Elsevier, London, UK.

Kéry, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications 15:1450–1461.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39.

MacKenzie, D., and L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

Madden, E., and R. Murphy. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144:377–392.

Marc J. Mazerolle. 2016. AICcmodavg: model selection and multimodel inference based on (Q)AICc. R package version 2.0-4. http://CRAN.R-project.org/package=AICcmodavg. Accessed 1 April 2016.

McMaster, D. G., J. H. Devries, and S. K. Davis. 2005. Grassland birds nesting in haylands of southern Saskatchewan : landscape influences and conservation priorities. Journal of Wildlife Management 69:211–221.

Omernik, J. M. 1987. Map supplement: ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118–125.

Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American breeding bird survey 1966-1996. Studies in Avian Biology 19:27–44.

Rahmig, C. J., W. E. Jensen, and K. A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. Conservation Biology 23:420–32.

Robel, R. J., J. P. Hughes, S. D. Hull, K. E. Kemp, and D. S. Klute. 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management 51:132–138.

Rollfinke, B. F., and R. H. Yahner. 1990. Effects of time of day and season on winter bird counts. Condor 92:215–219.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Rubin, D. B. 1976. Inference and missing data. Biometrika 63:581–592.

Rushing, C. S., T. B. Ryder, P. P. Marra, and C. S. Rushing. 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. Proceedings of the Royal Society B: Biological Sciences 283:20152846.

Scheiman, D. M., E. K. Bollinger, and D. H. Johnson. 2003. Effects of leafy spurge infestation on grassland birds. Journal of Wildlife Management 67:115–121.

Sutter, B., and G. Ritchison. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology 76:345–351.

Thompson, S. J., T. W. Arnold, and C. L. Amundson. 2014. A multiscale assessment of tree avoidance by prairie birds. Condor 116:303–315.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. American Midland Naturalist 91:195–213.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1–93.

Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland nesting birds. Conservation Biology 13:1424–1436.

Winter, M., and D. Johnson. 2004. Nesting biology of three grassland passerines in the northern tallgrass prairie. Wilson Bulletin 116:211–223.

Winter, M., D. H. Johnson, J. Shaffer, and A. 2005a. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

Winter, M., J. a. Shaffer, D. H. Johnson, T. M. Donovan, W. D. Svedarsky, P. W. Jones, and B. R. Euliss. 2005b. Habitat and nesting of le conte's sparrows in the northern tallgrass prairie. Journal of Field Ornithology 76:61–71.

Winter, M., D. Johnson, J. Shaffer, M. Therese, and D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70:158–172.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag. New York, USA.

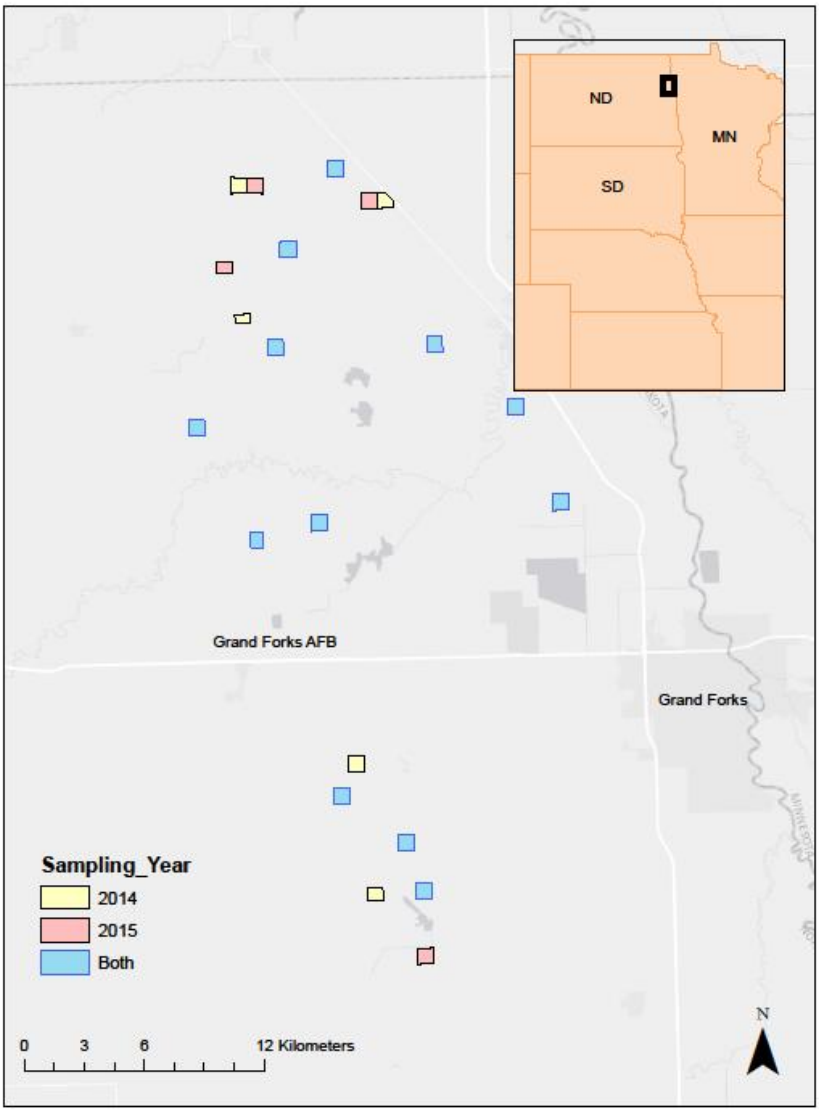

Figure 1. Map of sampling locations throughout Grand Forks County, ND. Colored polygons represent the sites sampled, with colors denoting the years sampled. Dark grey polygons represent water features, and light grey polygons city limits. Square in the inset shows location of the study area in the Midwestern United States.

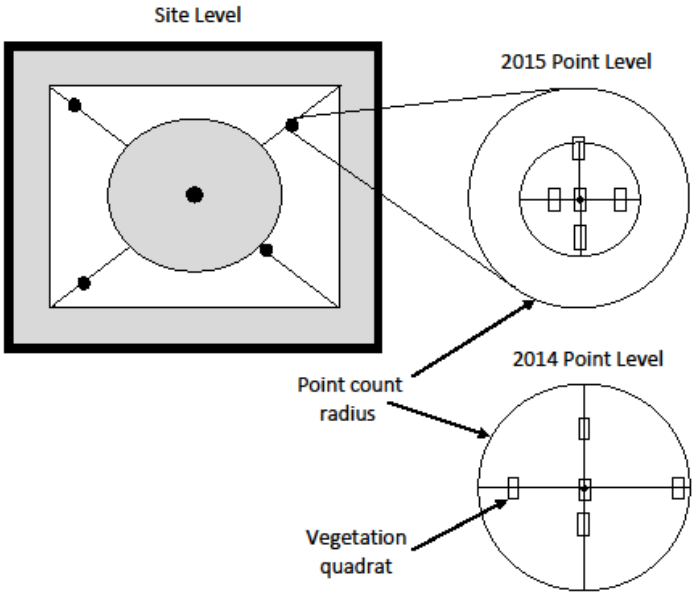

Figure 2. . Diagram illustrating the sampling framework. Bird points (solid black dots) were randomly placed within sampling sites (large square) after accounting for a 150 m edge buffer (shaded grey area). The inner grey circle denotes a 225 m buffer from the central sampling point, thin lines extending from the central circle represent the bounds within which the remaining 4 sampling points were placed within square sites. ,. Each bird point consisted of a 200 m diameter circle (100 m detection radius; inset circles). In 2015, vegetation quadrats (rectangles) were located within 50 m of the center of each detection radius. In 2014 vegetation quadrats were located within the entire 100 m detection radius. .

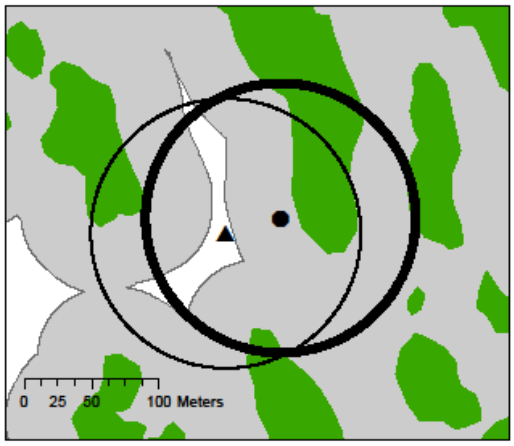

Figure 3. Illustration of the 2015 point replacement procedure for any 2014 points falling in a wetland or within 50 m of a wetland. Green=wetland. Grey=50 m buffer. A 2014 point (circle; bold radius) was replaced by a 2015 point (triangle; thin radius) that fell outside of a 50m buffer around wetland areas.

Table1. Candidate models for the full habitat model selection process. Number of shrubs and trees (WOODY) was log transformed for both years. Bare ground coverage (BARE) was log transformed for 2014. VOR=visual obstruction reading (cm), LIVEHT=live vegetation height (cm), LITDEP=litter depth (cm), SD=standard deviation.

Model Name	Covariates
Null	None
Detection	Best model from detection covariate selection (DATE, TIME, WIND)
Structure	Detection + Best model from vegetation structure model selection (VOR, LITDEP, LIVEHT, or SD)
Bare	Detection + BARE
Grass	Detection + GRASS
Woody	Detection + WOODY
Structure + Bare	Detection + Structure + BARE
Structure + Grass	Detection + Structure + GRASS
Structure + Woody	Detection + Structure + WOODY
Full	Detection + Structure + BARE + GRASS + WOODY

Table 2. Candidate models for the vegetation structure model selection process. VOR=visual obstruction reading (cm), LIVEHT=live vegetation height (cm), LITDEP=litter depth (cm), SD=standard deviation.

Model	Covariates
Null	None
Det	Best model from detection covariate selection (DATE, TIME, WIND)
3	Det+VOR
4	Det+VOR+VOR^2
5	Det+VORSD
6	Det+VORSD+VORSD^2
7	Det+LIVEHT
8	Det+LIVEHT+LIVEHT^2
9	Det+LIVEHTSD
10	Det+LIVEHTSD+LIVEHTSD^2
11	Det+LITDEP
12	Det+LITDEP+LITDEP^2
13	Det+LITDEPSD
14	Det+LITDEPSD+LITDEPSD^2

Table 3. Results from a one-way ANOVA with Welch's correction for unequal variance testing effects of management type (hayed, grazed, idle) on mean vegetation measures. F=F statistic, df=degrees of freedom (numerator, denominator), p=p-value

	2014			2015		
Vegetation	F	df	p	F	df	p
VOR	3.09	2.00, 17.17	0.07	10.13	2.00, 24.67	<0.0001
LIVEHT	2.98	2.00, 12.44	0.09	2.74	2.00, 21.54	0.09
LIT	2.68	2.00, 11.73	0.11	3.04	2.00, 27.48	0.06
WOODY	4.02	2.00, 16.69	<0.05	4.32	2.00, 31.30	<0.05
GRASS	4.18	2.00, 17.05	<0.05	2.07	2.00, 26.49	0.15
BARE	1.12	2.00, 15.66	0.35	15.24	2.00, 32.28	<0.0001

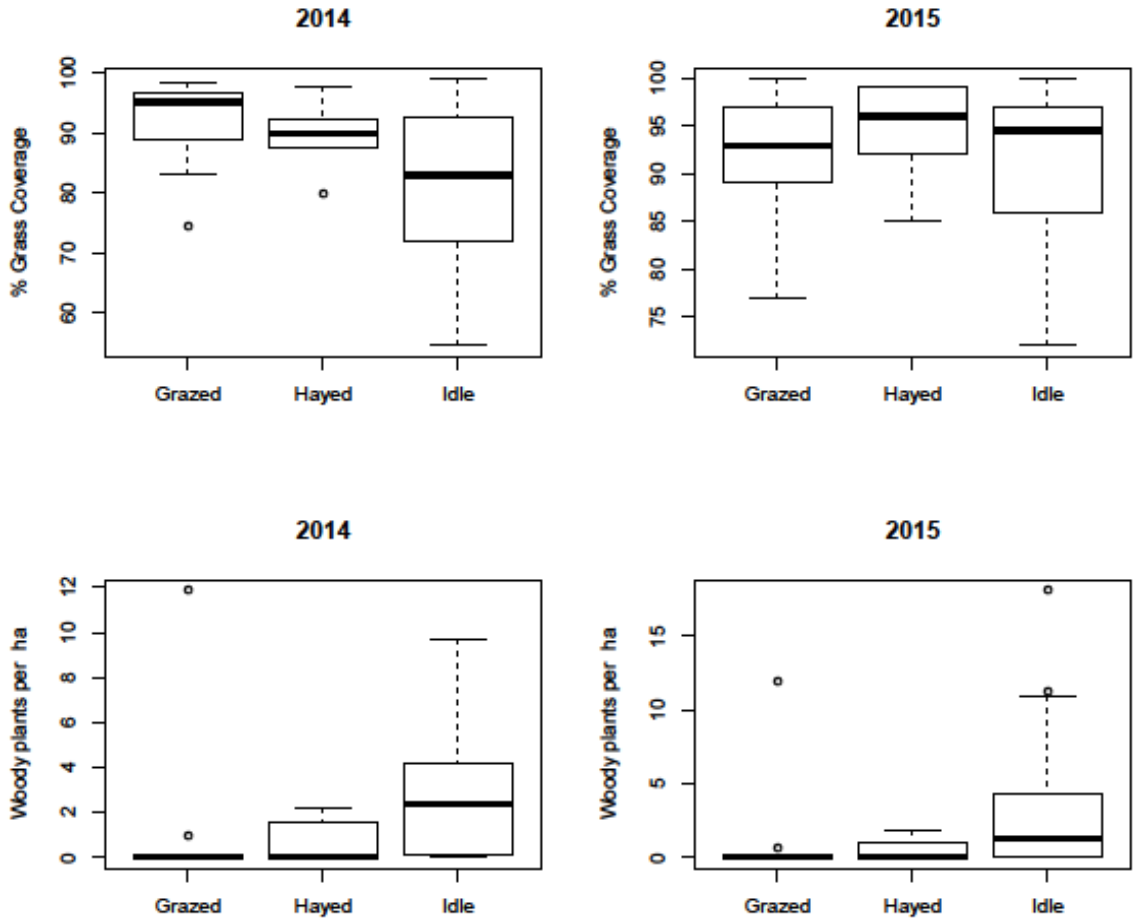

Figure 4**.** Boxplots of annual percentage of grass coverage and woody plants per ha at bird points in grazed, hayed and idle sites. Upper and lower box bounds represent 75th and 25th percentiles, whiskers are maximum and minimum values and dots outliers.

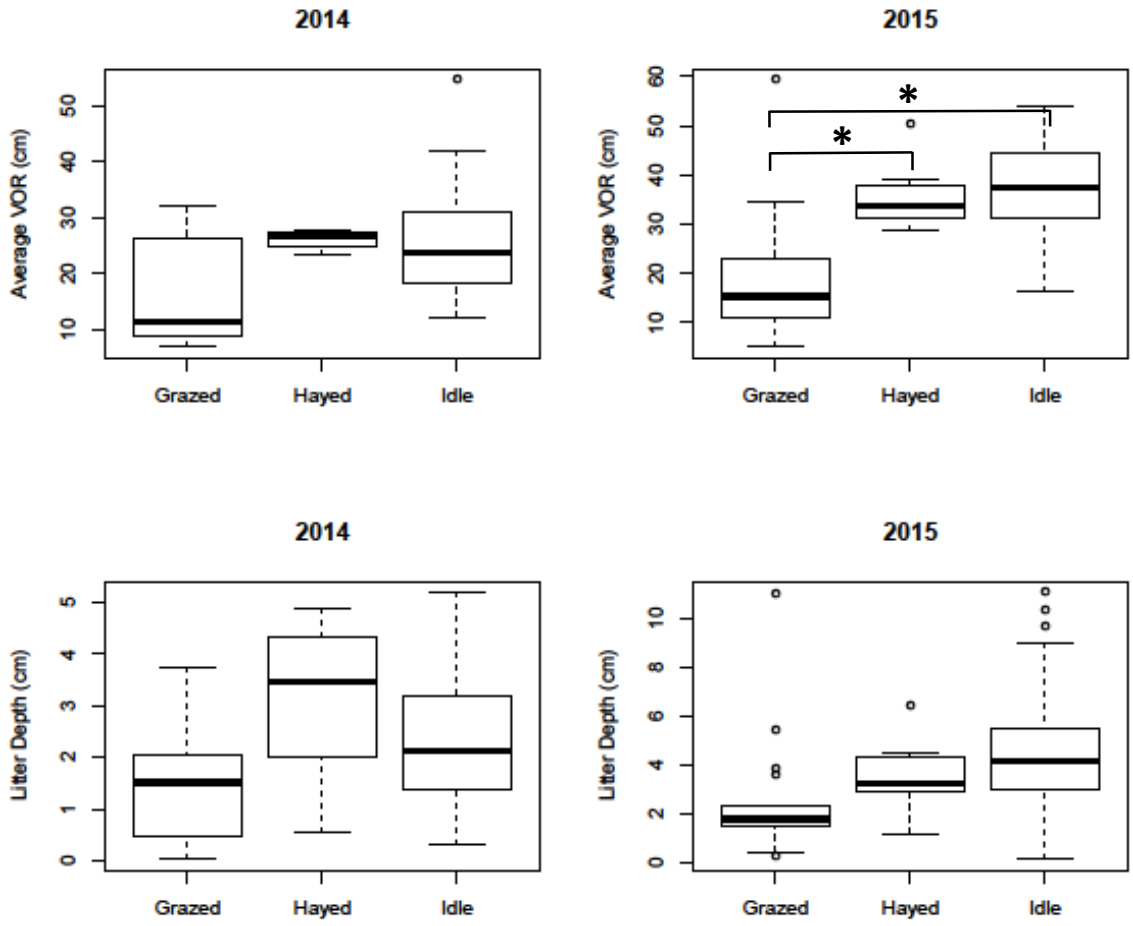

Figure 5. Boxplots of visual obstruction reading and litter depth in 2014 and 2015 at bird points in grazed, hayed and idle sites. Upper and lower box bounds represent 75th and 25th percentiles, whiskers are maximum and minimum values and dots outliers. Brackets above boxes represent groups with significant differences. *=significant difference with p-value <0.05.

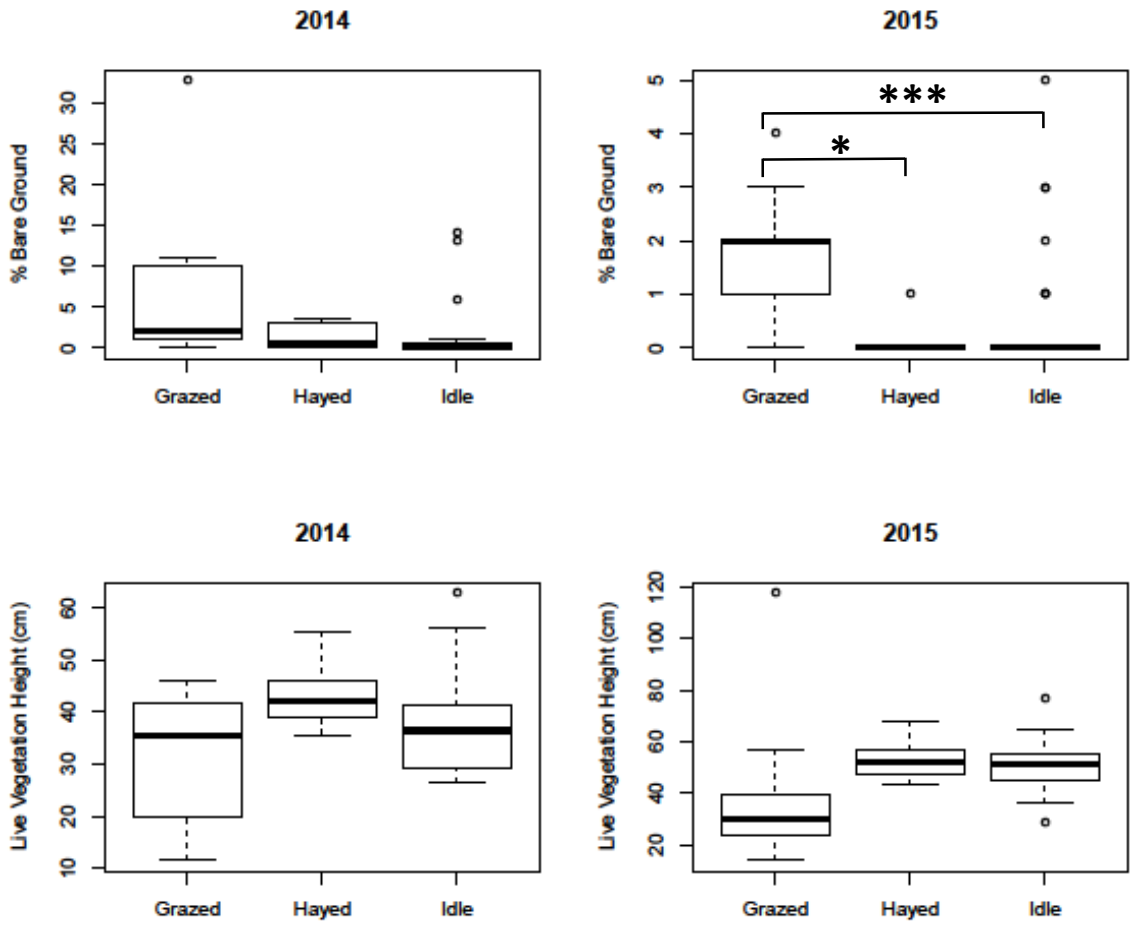

Figure 6. Boxplots of percentage bare ground and live vegetation height in 2014 and 2015 at bird points in grazed, hayed and idle sites. Upper and lower box bounds represent 75th and 25th percentiles, whiskers are maximum and minimum values and dots outliers. Brackets above boxes represent groups with significant differences. *=significant difference with p-value <0.05. ***=significant difference with p-value <0.0001.

Table 4**.** Top detection models for each bird species in each year. List of models was truncated at 2 ΔAIC for clarity. Models selected as most parsimonious are bolded and k is the number of model parameters. DATE= day of season, TIME= hours after sunrise, WIND= Beaufort scale wind speed.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	8	DATE+WIND	0.00	8	TIME+DATE	0.00
	7	**DATE**	**0.10**	**7**	**DATE**	**0.90**
	9	ALL	1.80	9	ALL	1.98
	8	TIME+DATE	1.94	-	-	-
Clay-colored Sparrow	**7**	**DATE**	**0.00**	**7**	**WIND**	**0.00**
	8	DATE+WIND	0.45	8	TIME+WIND	0.48
	8	TIME+DATE	1.37	8	DATE+WIND	0.87
	7	WIND	1.50	-	-	-
Le Conte's Sparrow	-	-	-	**7**	**TIME**	**0.00**
	-	-	-	8	TIME+DATE	1.70
	-	-	-	8	TIME+WIND	1.82
Savannah Sparrow	7	DATE	0.00	8	TIME+DATE	0.00
	6	**NULL**	**0.37**	**7**	**DATE**	**0.06**
	8	TIME+DATE	1.76	9	ALL	1.75
	7	TIME	1.86	8	DATE+WIND	2.05
	8	DATE+WIND	1.88	-	-	-
Sedge Wren	**8**	**TIME+DATE**	**0.00**	**8**	**TIME+WIND**	**0.00**
	9	ALL	1.92	9	ALL	2.00
Western Meadowlark	**6**	**NULL**	**0.00**	**7**	**TIME**	**0.00**
	7	WIND	1.06	8	TIME+DATE	1.44
	7	DATE	1.08	8	DATE+WIND	1.86
	7	TIME	1.99	-	-	-

Table 5. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Bobolink and Clay-colored Sparrow for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate of zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Covariates are defined in Table 1.

Covariates	Bobolink				Clay-colored Sparrow			
	2014		2015		2014		2015	
	β	SE	β	SE	β	SE	β	SE
Detection								
Intercept (p)	-0.81	0.44	-0.95	0.41	-0.92	0.49	0.05	0.25
DATE (p)	**-0.49**	0.12	**-0.27**	0.10	**0.27**	0.14	-	-
TIME (p)	-	-	-	-	-	-	-	-
WIND (p)	-	-	-	-	-	-	**-0.48**	0.15
Abundance								
Intercept (λ)	1.79	0.31	1.11	0.31	1.04	0.37	0.04	0.23
VOR (λ)	**0.38**	0.14	**0.63**	0.20	-	-	0.31	0.23
VOR^2 (λ)	**-0.35**	0.11	**-0.25**	0.12	-	-	-0.06	0.15
LIVEHT (λ)	-	-	-	-	-0.13	0.18	-	-
$LIVEHT^2$ (λ)	-	-	-	-	-0.57	0.33	-	-
LIT (λ)	-	-	-	-	-	-	-	-
LIT^2 (λ)	-	-	-	-	-	-	-	-
WOODY (λ)	-0.10	0.10	-0.11	0.12	**0.37**	0.10	**0.33**	0.11
GRASS (λ)	0.04	0.10	0.17	0.11	-0.09	0.14	**-0.34**	0.12
BARE (λ)	0.01	0.14	-0.32	0.21	-0.57	0.33	-0.28	0.27
CATTAIL (λ)	-	-	-	-	-	-	-	-

Table 6. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Le Conte's Sparrow and Savannah Sparrow for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate a zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Covariates are defined in Table 1.

	Le Conte's Sparrow				Savannah Sparrow			
	2014		2015		2014		2015	
	β	SE	β	SE	β	SE	β	SE
Detection								
Intercept (p)	-	-	-0.90	0.35	-1.52	1.32	1.25	0.13
DATE (p)	-	-	-	-	-	-	**0.34**	0.09
TIME (p)	-	-	**-0.81**	0.20	-	-	-	-
WIND (p)	-	-	-	-	-	-	-	-
Abundance								
Intercept (λ)	-	-	-0.38	0.27	2.85	1.10	1.25	0.13
VOR (λ)	-	-	**0.69**	0.21	-0.08	0.08	-	-
VOR^2 (λ)	-	-	-	-	**-0.15**	0.06	-	-
LIVEHT (λ)	-	-	-	-	-	-	-	-
$LIVEHT^2$ (λ)	-	-	-	-	-	-	-	-
LIT (λ)	-	-	-	-	-	-	-	-
LIT^2 (λ)	-	-	-	-	-	-	-	-
WOODY (λ)	-	-	-0.12	0.22	-0.07	0.08	-	-
GRASS (λ)	-	-	-0.16	0.16	-	-	-0.07	0.08
BARE (λ)	-	-	-0.24	0.33	0.08	0.07	0.01	0.10
CATTAIL (λ)	-	-	-	-	**-0.22**	0.08	0.00	0.10

Table 7. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Sedge Wren and Western Meadowlark for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate a zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Covariates are defined in Table 1.

	Sedge Wren				Western Meadowlark			
	2014		2015		2014		2015	
	β	SE	β	SE	β	SE	β	SE
Detection								
Intercept (p)	-1.10	0.52	0.16	0.23	-1.38	0.65	0.10	0.22
DATE (p)	**0.48**	0.16	-	-	-	-	-	-
TIME (p)	**-0.40**	0.15	-0.39	0.13	-	-	**-0.36**	0.12
WIND (p)	-	-	-0.37	0.12	-	-	-	-
Abundance								
Intercept (λ)	1.00	0.37	0.29	0.17	1.14	0.50	0.14	0.16
VOR (λ)	-	-	**1.18**	0.25	**-0.44**	0.10	**-0.60**	0.14
VOR^2 (λ)	-	-	**-0.34**	0.15	**0.24**	0.06	-	-
LIVEHT (λ)	**0.89**	0.24	-	-	-	-	-	-
$LIVEHT^2$ (λ)	**-0.27**	0.12	-	-	-	-	-	-
LIT (λ)	-	-	-	-	-	-	-	-
LIT^2 (λ)	-	-	-	-	-	-	-	-
WOODY (λ)	-0.06	0.14	-0.13	0.15	-	-	-0.05	0.13
GRASS (λ)	0.04	0.16	-0.02	0.11	**-0.22**	0.11	0.11	0.13
BARE (λ)	-0.11	0.25	0.13	0.22	-	-	0.12	0.13
CATTAIL (λ)	-	-	-	-	-	-	-	-

Table 8**.** Top models from the vegetation structure model selection process. List of models was truncated at <2 ΔAIC for clarity. Models that were selected as most parsimonious are bolded and k is the number of model parameters. VOR- visual obstruction reading (cm), LIT- litter depth (cm), LIVEHT- live vegetation height (cm). Any term that is squared also included a linear term in the model.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	**5**	**VOR²**	**0.00**	**7**	**VOR²**	**0.00**
	5	LIVEHT²	1.12	-	-	-
Clay-colored Sparrow	**5**	**LIVEHT²**	**0.00**	**4**	**VOR**	**0.00**
	5	VOR²	0.59	5	VOR²	0.56
	-	-	-	5	LITDEP²	1.49
	-	-	-	5	LIVEHT²	2.03
Le Conte's Sparrow	-	-	-	**5**	**LIVEHT²**	**0.00**
	-	-	-	5	LITDEP²	0.13
	-	-	-	4	VOR	1.27
	-	-	-	5	VOR²	1.30
Savannah Sparrow	**5**	**VOR²+CATTAIL**	**0.00**	**3**	**DETECTION**	**0.00**
	-	-	-	4	VOR	0.74
	-	-	-	4	LIVEHT	1.01
	-	-	-	4	LITDEP	1.06
	-	-	-	4	LITDEPSD	1.53
	-	-	-	4	LIVEHTSD	1.64
	-	-	-	4	VORSD	1.70
	-	-	-	5	VOR²	1.90
Sedge Wren	**6**	**LIVEHT²**	**0.00**	**6**	**VOR²**	**0.00**
Western Meadowlark	**4**	**VOR²**	**0.00**	**4**	**VOR**	**0.00**
	-	-	-	5	VOR²	1.21

Table 9. Top models from the final habitat model process. List of models was truncated at <2 ΔAIC for clarity. VOR= visual obstruction reading (cm), LIT=litter depth (cm), LIVEHT= live vegetation height (cm), BARE=bare ground coverage, GRASS=percent grass coverage, WOODY=sum of tree and shrub number, DETECTION=best detection model. Any term that is squared also included a linear term in the model.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	5	VOR^2	0.00	7	VOR^2+BARE	0.00
	6	VOR^2+WOODY	0.99	9	FULL	0.10
	6	VOR^2+GRASS	1.80	6	VOR^2	0.56
	6	VOR^2+BARE	1.94	7	VOR^2+WOODY	0.71
	-	-	-	7	VOR^2+GRASS	1.11
Clay-colored Sparrow	6	$LIVEHT^2$+WOODY	0.00	7	FULL (VOR)	0.00
	8	FULL	1.79	-	-	-
Le Conte's Sparrow	-	-	-	4	VOR	0.00
	-	-	-	5	VOR+GRASS	1.02
	-	-	-	5	VOR+BARE	1.41
	-	-	-	5	VOR+WOODY	1.65
Savannah Sparrow	5	VOR^2+WOODY	0.00	3	DETECTION	0.00
	4	VOR^2	0.93	4	WOODY	0.51
	5	VOR^2+BARE	1.69	4	BARE	1.99
	-	-	-	4	GRASS	2.00
Sedge Wren	6	$LIVEHT^2$	0.00	6	VOR^2	0.00
	7	$LIVEHT^2$+BARE	1.77	7	VOR^2+BARE	1.21
	7	$LIVEHT^2$+GRASS	1.94	7	VOR^2+WOODY	1.33
	7	$LIVEHT^2$+WOODY	1.97	7	VOR^2+GRASS	1.40
Western Meadowlark	5	VOR^2+GRASS	0.00	4	VOR	0.00
	4	VOR^2	1.67	5	VOR+BARE	1.21
	-	-	-	5	VOR+WOODY	1.33
	-	-	-	5	VOR+GRASS	1.40

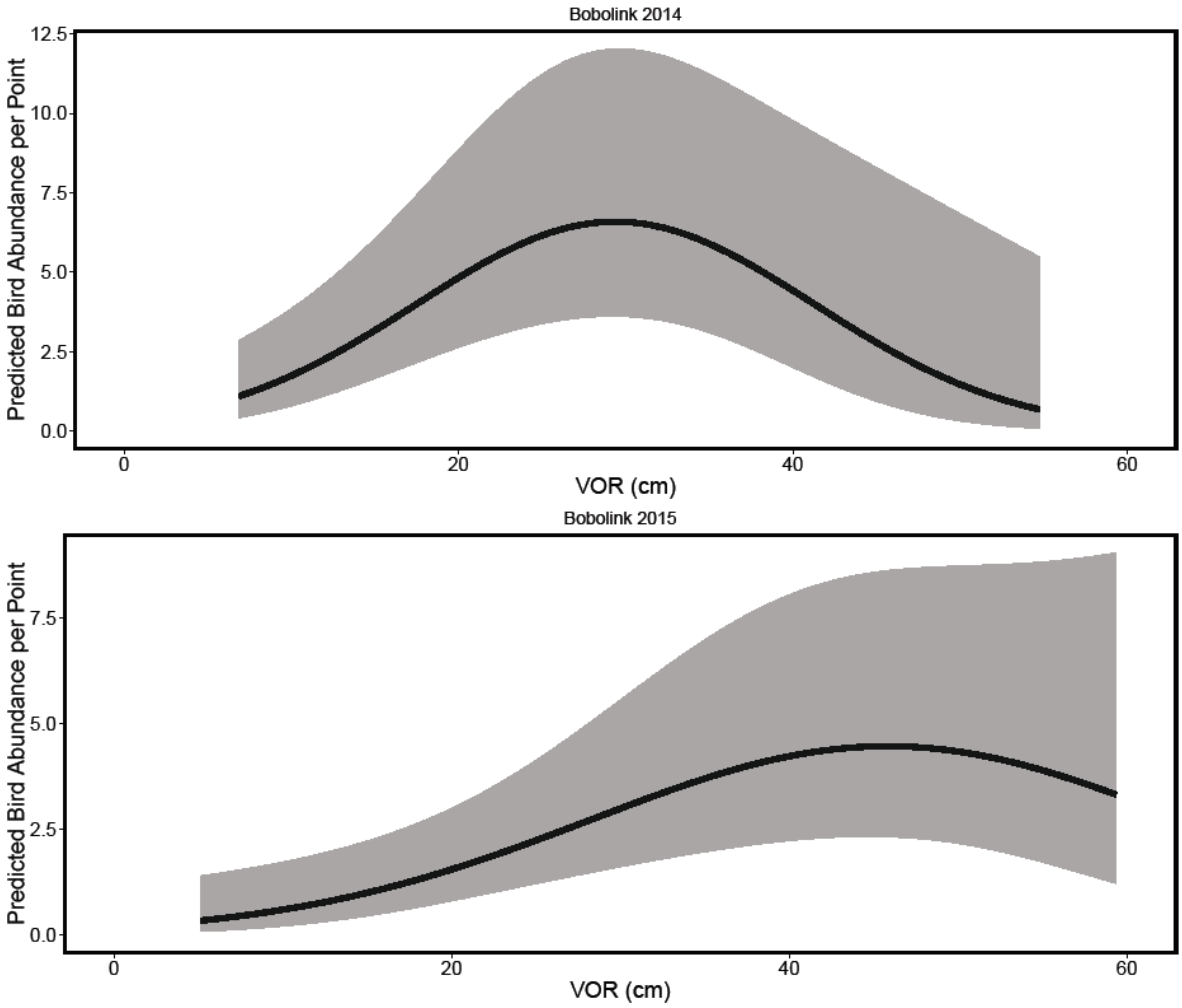

Figure 7. Predicted Bobolink abundance with 95% confidence intervals. The measure of vegetation on the x-axis was varied across all observed values, while all other covariates were held at their means. VOR= visual obstruction reading. Top plot is for 2014 and bottom for 2015.

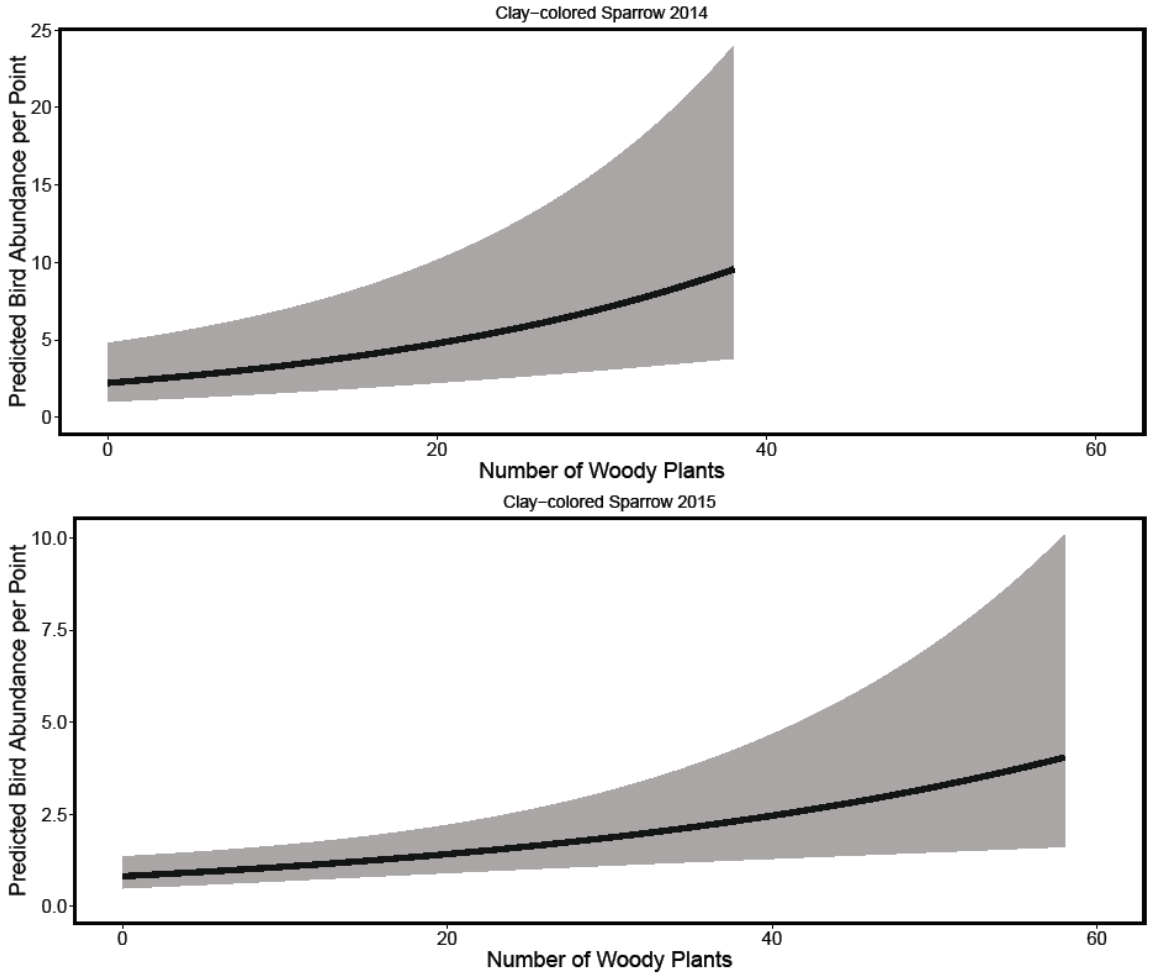

Figure 8. Predicted Clay-colored Sparrow abundance with 95% confidence intervals. The measure of vegetation on the x-axis was varied across all observed values, while all other covariates were held at their means. NOTE: Y-axes are not scaled equally. Top plot is for 2014 and bottom for 2015.

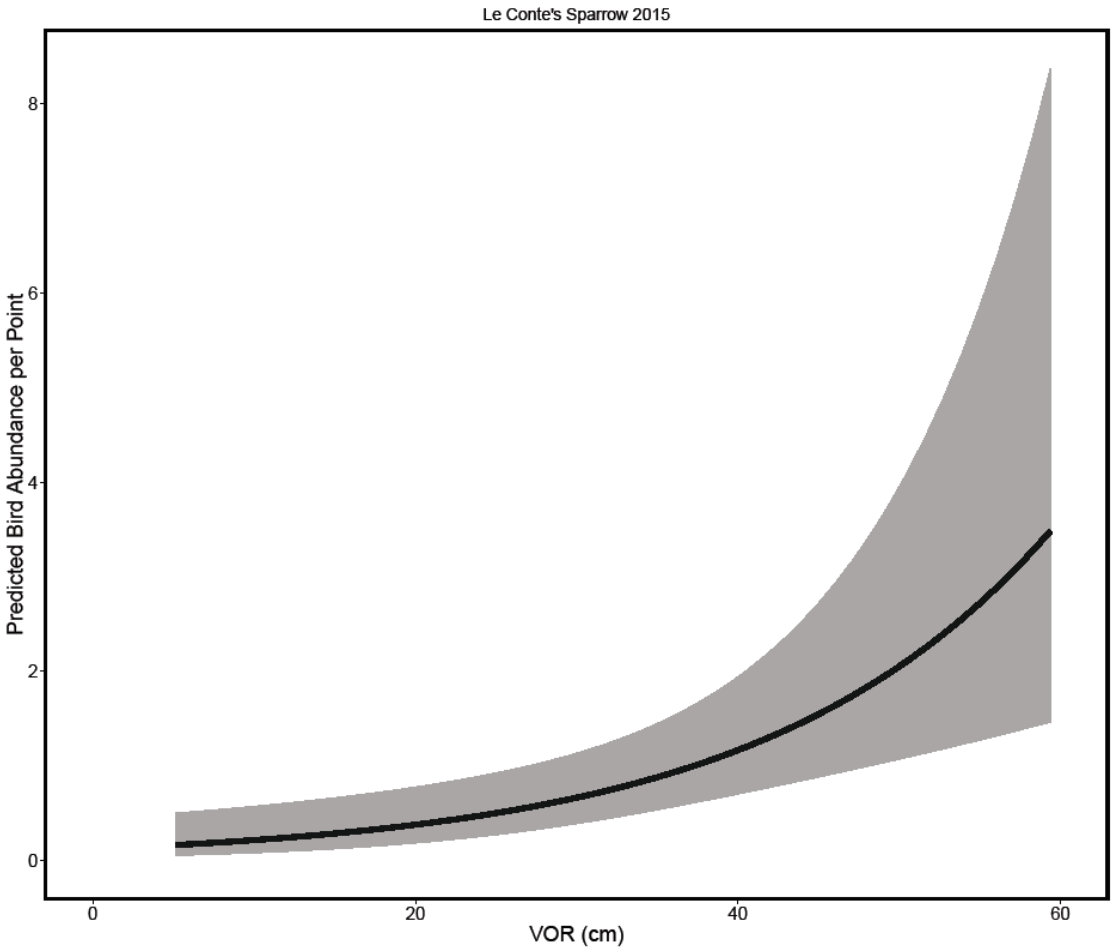

Figure 9. Predicted Le Conte's Sparrow abundance with 95% confidence intervals for 2015. The measure of vegetation on the x-axis was varied across all observed values, while all other covariates were held at their means. VOR= visual obstruction reading.

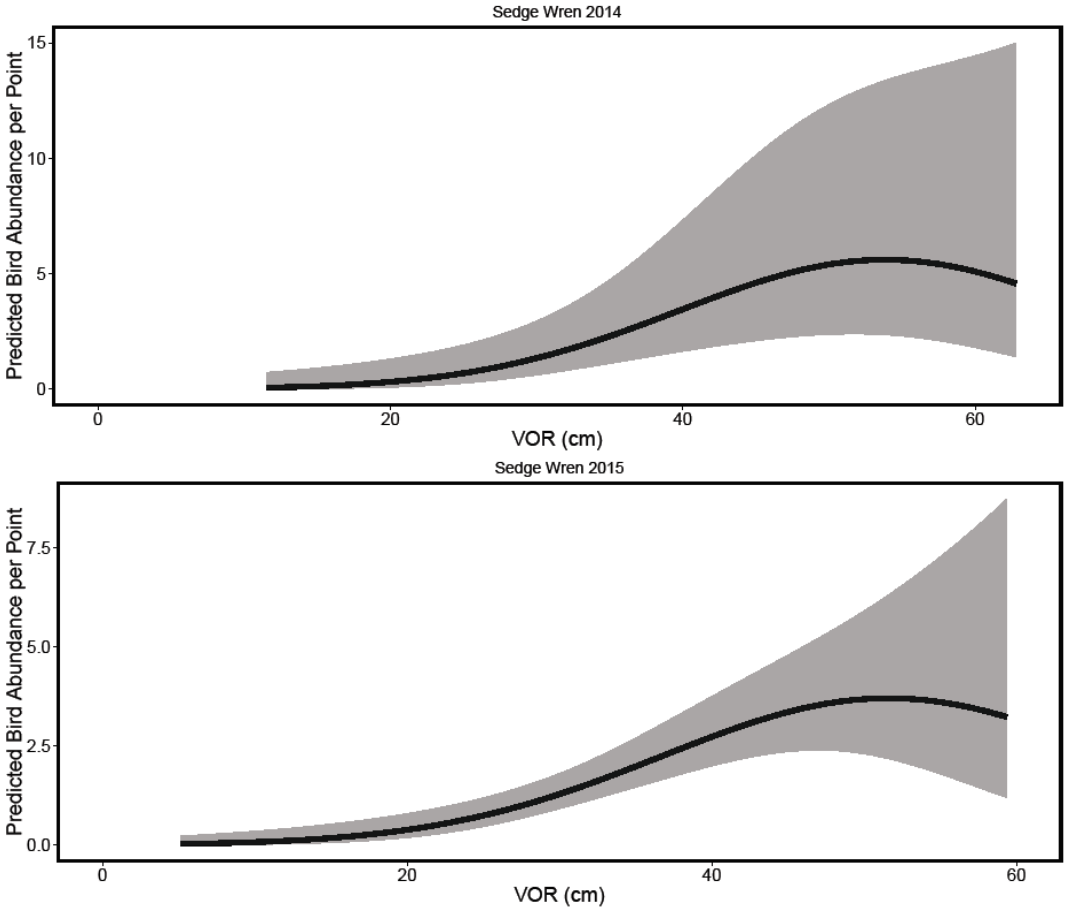

Figure 10. Predicted Sedge Wren abundance with 95% confidence intervals. The measure of vegetation on the x-axis was varied across all observed values, while all other covariates were held at their means. VOR= visual obstruction reading. NOTE: Y-axes are not scaled equally. Top plot is for 2014 and bottom for 2015.

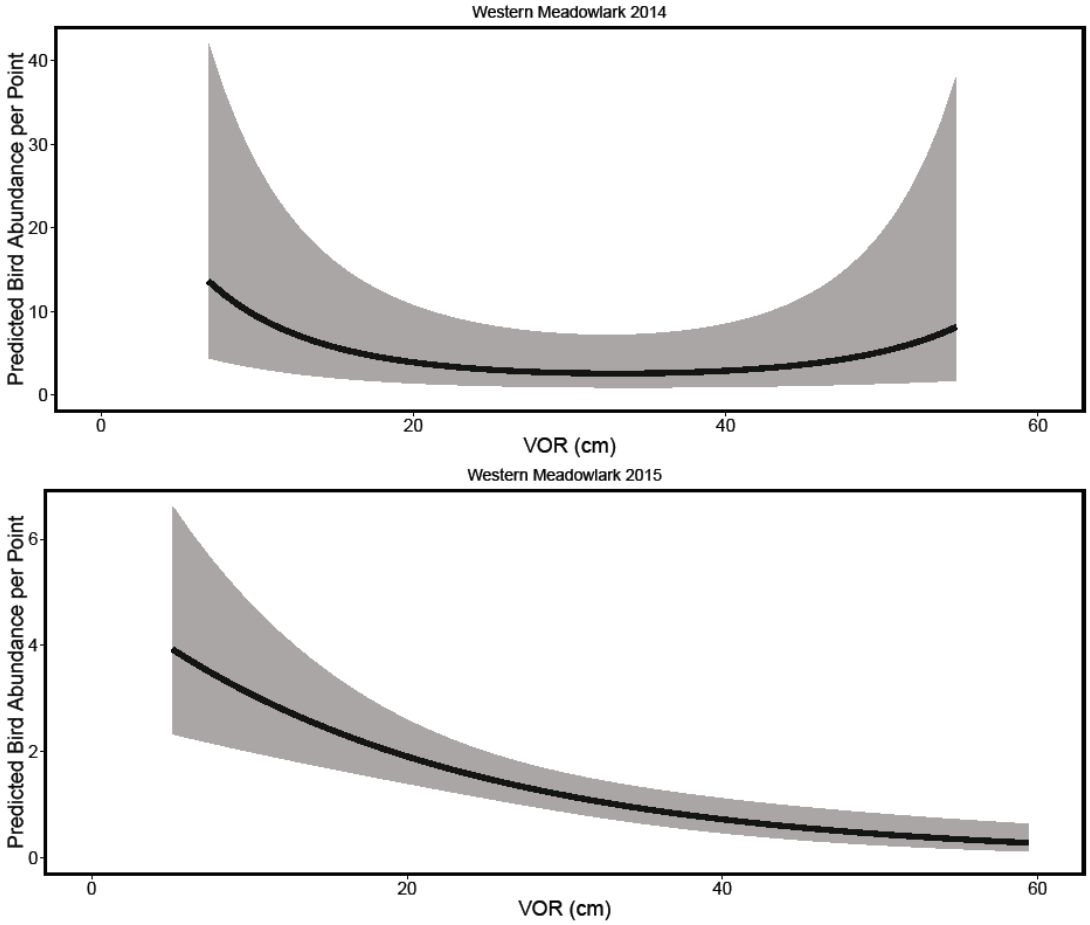

Figure 11. Predicted Western Meadowlark abundance with 95% confidence intervals. The measure of vegetation on the x-axis was varied across all observed values, while all other covariates were held at their means. VOR= visual obstruction reading. NOTE: Y-axes are not equally scaled. Top plot is 2014 and bottom for 2015.

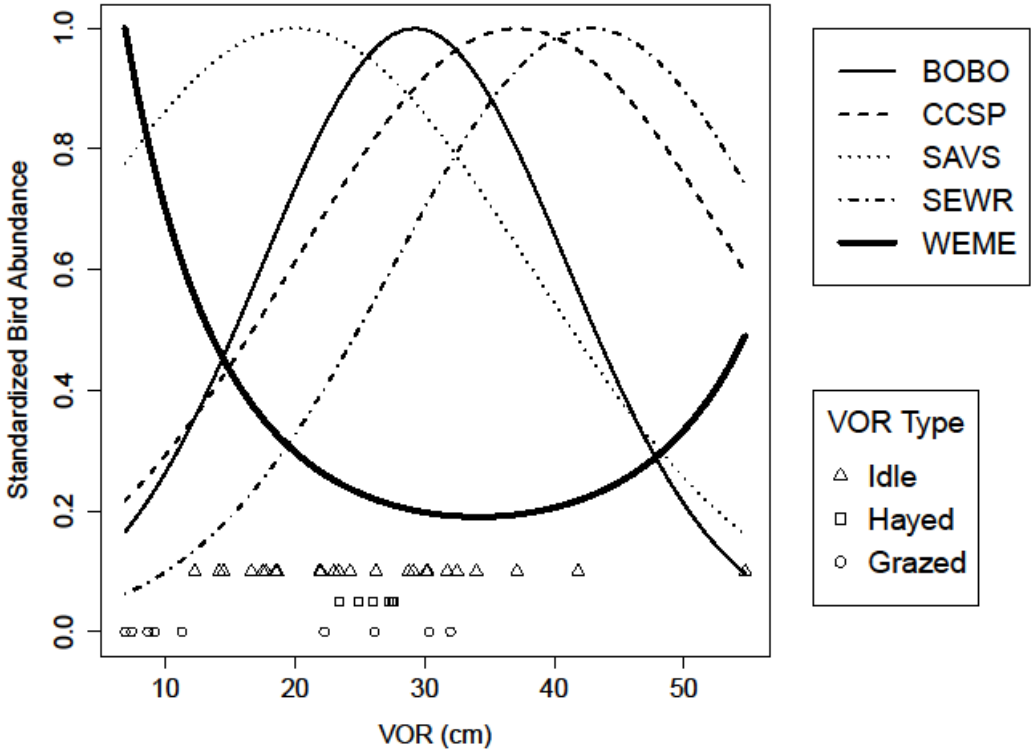

Figure 12. Standardized predicted bird abundance relative to VOR in 2014, with entire range of measured VOR values displayed. Codes for each bird species are as follows: BOBO-Bobolink, CCSP-Clay-colored Sparrow, SAVS- Savannah Sparrow, SEWR-Sedge Wren, WEME-Western Meadowlark. Dots below the plot of abundance, represent range of VOR measured on hayed, grazed and idle sites.

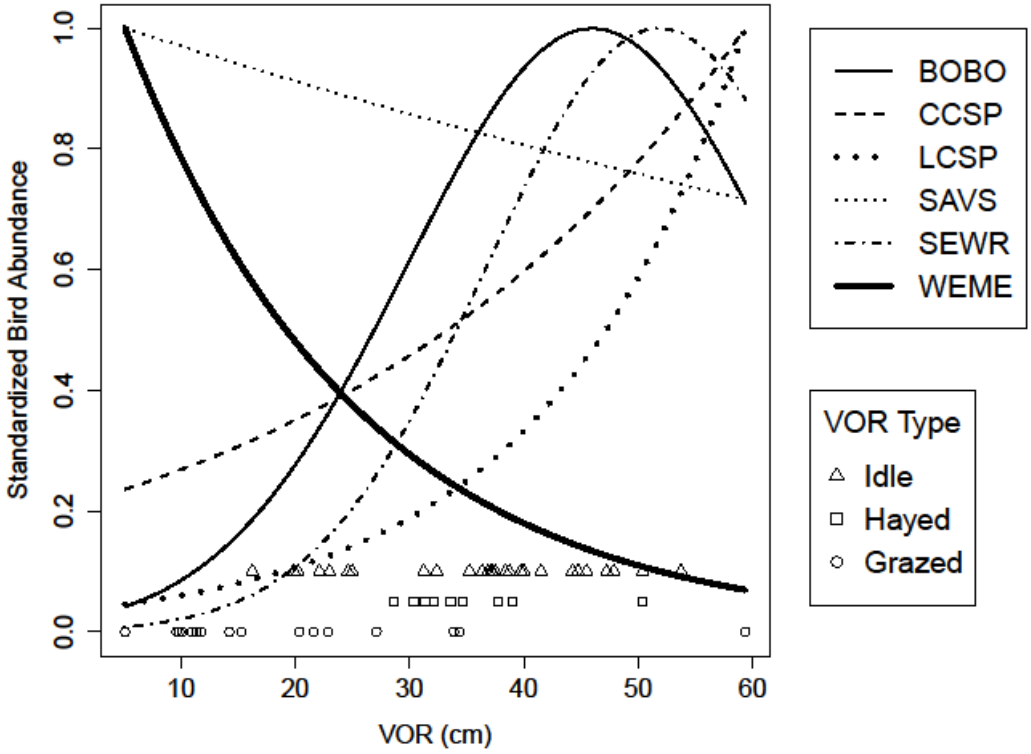

Figure 13. Standardized predicted bird abundance relative to VOR in 2015, with range of measured VOR values displayed. Codes for each bird species are as follows: BOBO-Bobolink, CCSP-Clay-colored Sparrow, LCSP-Le Conte's Sparrow, SAVS- Savannah Sparrow, SEWR-Sedge Wren, WEME-Western Meadowlark. Dots below the plot of abundance, represent range of VOR measured at hayed grazed and idle sites.

CHAPTER III

THE EFFECT OF LATE-SEASON PRESCRIBED BURNING ON GRASSLAND BIRDS IN A REMNANT TALLGRASS PRAIRIE

Abstract

Grasslands are one of the most imperiled ecosystems in North America and birds that use this habitat have shown some of the most consistent and widespread declines of any avian species. This decline highlights the need for effective management of remaining grassland for the maximum benefit of grassland birds. To generate the mosaic of vegetation structure required by multiple bird species, managers can use rotational prescribed burning which increases within site heterogeneity depending on time since burning. The objective of this study was to examine how grassland birds and vegetation structure respond to dormant season (fall) prescribed fire. Additionally, the effect of vegetation structure on the six most abundant bird species was examined with hierarchical modeling in both pre-burn (2014) and post-burn (2015) years. A remnant tallgrass prairie that was without any form of management for >30 years was divided into 7 management units, two of these units were burned in fall 2014. The bird and plant communities were surveyed during the summer in both years at 37 point count locations distributed evenly throughout the site. Only two measures of vegetation were significantly affected after prescribed burning, live vegetation height and litter depth both declined. In the pre-burn year vegetation density (VOR) was the most

important vegetation measure for four of five birds, and two of five birds in the post-burn year. Bobolink and Sedge Wren density declined in burned units and Western Meadowlark abundance increased. Two of the species that responded to burning had the strongest predictor of bird abundance shift from VOR during the pre-burn year to litter depth the post-burn year, suggesting that these species may use litter depth as an indicator of disturbance level. When controlling for differences in vegetation structure between burned and unburned units, I found no significant change in bird abundance between treatments, indicating that bird abundance may be responding to changes in vegetation structure generated by prescribed burning. These results suggest that initial prescribed burning of tallgrass prairie after decades of being idle may do little to alter the structure of the plant community, although some grassland bird species do respond immediately to burning.

Introduction

Grasslands are one the most threatened ecosystems in North America, with less than 4% of native tallgrass prairie remaining (Samson and Knopf 1994). Birds that depend on grassland habitat have shown similar dramatic declines within the last five decades, declining by 37.8% from 1968-2011 (Sauer et al. 2013) primarily because of this large-scale habitat loss within their breeding range. Grasslands have been rapidly converted to row-crop agriculture production in recent years in the Midwest, with a net loss of 530,000 ha from 2006-2011 in North Dakota, South Dakota, Nebraska, Minnesota and Iowa (Wright and Wimberly 2013). Most remaining grassland habitat is of relatively poor quality for grassland birds due to the negative effects of increasing

woody vegetation, habitat fragmentation, and grassland vegetation homogenization (Brennan and Kuvelsky 2005). In order to maintain grassland bird populations, grasslands must be managed to maximize their benefit to multiple bird species, especially in the Midwestern United States.

Most research on generating beneficial habitat for grassland birds has been focused on patch-burn grazing (e.g., Hovick et al. 2015, Hovick et al. 2014, Weir et al. 2013, Hovick et al. 2012, Coppedge et al. 2008, Fuhlendorf et al. 2006), since it generates a mosaic of habitat structure that is beneficial to multiple grassland bird species (Fuhlendorf et al. 2006). Patch-burn grazing is the rotational burning of management units within a prairie complex and allowing cattle to preferentially graze recently burned areas, while leaving unburned units to recover (Fuhlendorf et al. 2009). Without management, grassland patches become less suitable for a full suite of grassland birds, since these areas have dense vegetation with increased woody plant abundance, precluding their use by birds that prefer sparser more open habitat. Relative to patch-burn grazing, there has been less study of grassland bird response to prescribed burning (e.g., Long et al. 2014, Grant et al. 2012, Grant et al. 2010), the deliberate burning of grassland to meet management objectives, even though burning is widely used. There are 10,000-20,000 ha of national wildlife refuges in the Dakotas and eastern Montana burned annually (Grant et al. 2012).

Among the few studies that examine just the effect of prescribed burning on grassland bird abundance, there are even fewer conducted in North Dakota. The majority of work on prescribed burning and grassland birds in North Dakota has been

done in the northern mixed-grass prairie ecosystem (Madden et al. 2000, Grant et al. 2010, Grant et al. 2012). Many studies that examine the effect of prescribed burning, or grazing and burning, have been conducted in the southern tallgrass prairie, primarily on Konza Prairie in Kansas (e.g. Hovick et al. 2012, Hovick et al. 2014). Both mixed-grass and southern tallgrass prairie regions have dramatically different climatic and precipitation regimes than the northern tallgrass prairie, with southern tallgrass prairie receiving some of the highest amounts of rainfall of any grassland region in the U.S. (Laurenroth et al. 1999) and due to high rainfall and temperature southern prairie is dominated by taller grasses. It is difficult to generalize effects of prescribed burning on bird abundance between ecoregions, since bird species have been shown to vary their habitat associations presumably due to climate and precipitation differences between ecoregions (Baaker et al. 2002). Therefore, it is imperative to examine the responses of vegetation and birds to management in the northern tallgrass prairie.

My objectives were to evaluate the short-term effects of fall burning on a remnant northern tallgrass prairie, on the structure of the vegetative community and the avian community. I used an *N*-mixture modeling framework (Royle et al. 2004) to account for imperfect detection of birds and examine any shift in relationships between bird abundance and vegetation structure before and after prescribed burning. Any bird species that showed a significant change in abundance between burned and unburned units in the post-fire year were further examined. By accounting for imperfect detection and vegetation structure we can glean a better understanding of how fire changes

vegetation structure and subsequently changes bird abundance, giving managers specific vegetation measures to target for habitat improvement

Methods

Study Area

This study took place on Oakville Prairie Field Station (hereafter Oakville) in Grand Forks County, North Dakota (Centroid: -97.315585 °W, 47.906469 °N). The native plant species with the greatest cover were foxtail barley (*Hordeum jubatum*), prairie cordgrass (*Spartina pectinata*), common ragweed (*Ambrosia artemisiifolia*), and the non-native plants Smooth brome (*Bromus inermis*), Canada thistle (*Cirsium arvense*) and Kentucky bluegrass (*Poa pratensis*). The dominant woody species were Western snowberry (*Symphoricarpos occidentalis),* prairie rose (*Rosa arkansana*), and Russian olive (*Elaeagnus angustifolia*). In 2014 annual precipitation was 55.91 cm and mean temperature of 8.8°C, ranging from -16.8°C in January, to 19.9°C in August (National Oceanic and Atmospheric Administration [NOAA] 2014). Annual weather summaries are not yet available for 2015. After more than 30 years without any form of disturbance on Oakville, the site was divided into 7 management units, with two units burned in early October 2014 (Figure 14).

Bird Survey Point Placement

Bird survey points (bird points) were chosen from an established set of vegetation-sampling points situated in a 100 m grid within each management unit (Figure 14). A grid with points spaced 200 m apart was placed on top of the existing vegetation-sampling grid (Figure 15) beginning at the most NW vegetation-sampling point. I used a 200 m grid to ensure that bird points did not have overlapping 100 m survey radii. The most central location of the bird point grid (grey point in Figure 15) was selected for inclusion to give a representative sample of the center of each management unit. The remaining portions of each management unit were divided into sections (rectangles in Figure 15). One bird point was selected from each section for inclusion. The number of bird points selected was proportional to each management unit's area, ranging from 4-6. A total of 37 bird points were surveyed at Oakville (Figure 14), with 11 in burned units and 26 in unburned units.

Bird Survey

Oakville was surveyed from June 3-July 5 2014 (pre-burn) and May 28-June 29 2015 (post-burn). Surveys began at local sunrise ~0530, as determined by the U.S. Naval Observatory for Grand Forks, ND, and continued until 1000. No locations were surveyed during high wind (>4 Beaufort scale), rain, or heavy fog (Winter et al. 2006). Bird points were visited 3 times with surveys ~9 days apart in 2014 and 4 times with surveys ~10 days apart in 2015. The season's weather conditions dictated the maximum number of visits possible to each survey point. The bird point visit order was

alternated to ensure an early (~0530-0700), mid (0700-0830), and late (0830-1000) morning visit for each point.

Upon arrival at each bird point, I observed a two-minute rest period (cool-down) to allow birds to return to their positions prior to my arrival. During cool-down, I recorded wind speed, estimated by using the Beaufort scale, time of day, and day of the season. The data recorded during cool-down were later used as detection covariates, variables that could influence the chance of observing a bird species during an individual visit. Immediately following cool-down, all birds were recorded for 5-min, noting all birds seen or heard within a 100 m detection radius (Bibby et al. 2000). Birds were only counted if they were using the habitat in the detection radius, meaning those on the ground or perched on vegetation. Any birds flying over the detection radius were recorded as a flyover and were excluded from analysis. The counts of visual detections of males, or males and females for species that are not sexually dimorphic, and singing birds were summed and used as abundance measures for each species.

Vegetation Survey

Local vegetation structure and composition was measured in early July each season. This time period was chosen because vegetation measurements from later in the breeding season have been found to be better predictors of bird abundance (Winter and Faaborg 1999). The first year, five vegetation quadrats (0.5 × 1.0 m) were randomly placed within each detection radius. The first quadrat was placed in the center of the bird point and four quadrats placed a random distance >15 m from the central quadrat

within the detection radius using ArcGIS 10.1 (ESRI, Redlands, California, USA). In 2015 vegetation quadrats were placed within 50 m of the central bird point using the same methodology as 2014.

Non-overlapping aerial percent cover was estimated to the nearest 5% for forbs, grasses (graminoids), and woody plant species within each vegetation quadrat. Bare ground was defined as any soil not obscured by vegetation or litter, and was estimated to the nearest 5%. Visual obstruction was measured in 2.5 cm increments in the center of the quadrat, from a distance of 4 m and a height of 1.5 m, in each cardinal direction using a Robel pole (Robel et al. 1970). Measurements of vegetation height (nearest 0.1 cm) and litter depth (nearest 0.1 cm) followed those outlined by Winter et al. (2004). The number of shrubs (< 1 m tall) and trees (> 1m tall) within the detection radius were recorded. I averaged all vegetation measurements from the five quadrats to describe the vegetation structure and composition for each bird point. Variability of vegetation at each bird point was calculated by taking the SD of the five quadrats. Counts of trees and shrubs were combined for each bird point to generate an index of woody vegetation.

Vegetation Structure Change Analysis

I used a Welch's t-test to determine whether there was a significant change in any measure of vegetation after burning. The measure of change in vegetation structure between burned and unburned units was the difference in the mean vegetation measure for each bird point. For example, change in VOR for a bird point was calculated

by subtracting the mean VOR for that point in 2015 from the mean VOR for the same point in 2014. Additionally, I tested mean VOR, live vegetation height, and litter depth for correlation to each other within each year to determine if these measures of structure were indeed correlated as has been observed in other grassland studies. Those same measures of vegetation were tested for correlation between years. For example, VOR from 2014 was tested for correlation with VOR in 2015.

Bird Abundance Analysis

The bird abundance analysis was restricted to the six most abundant grassland bird species (>60 detections) because sparse observations of birds could lead to large uncertainty in abundance estimates (Kéry and Royle 2016). Of the species analyzed, two are Species of Conservation Priority (SoCP) for North Dakota (Dyke et al. 2015): Bobolink (*Dolichonyx oryzireus*) and Western Meadowlark (*Sturnella neglecta*). Three non-SoCP bird species, Clay-colored Sparrow (*Spizella pallida*) and Savannah Sparrow (*Passerculus sandwichensis*), and Sedge Wren (*Cistothorus platensis*), were also included.

The *N*-mixture modeling framework (Royle et al. 2004) in program R (R Core Team 2014) with package 'unmarked' and module 'pcount' (Fiske and Chandler 2011) was used to account for imperfect detection. This analysis simultaneously considers the influence of detection covariates (e.g. time of day) on detection probability and vegetation covariates (e.g. litter depth) on bird abundance (Royle et al. 2004). It is important to incorporate detection probability when modeling bird abundance, since most bird species are not detected at the same rate throughout a season or time of day

(Rollfinke and Yahner 1990). Once variation in counts due to detection probability is accounted for, the effect of vegetation covariates can be modeled. The aim of using *N*-mixture modeling was to determine which measures of vegetation have the greatest effect on bird abundance, when accounting for all sources of variation (i.e. detection). Additionally, I wanted to evaluate whether the vegetation covariates that best predicted bird abundance changed from the pre-fire year to the post-fire year for bird species that showed a significant response to burning. Presumably the vegetation measures chosen as the best explanatory variables for bird abundance in the year after burning are what birds use as indicators of habitat suitability after a disturbance.

An assumption of the *N*-mixture model is a closed population, meaning no immigration or emigration during the entirety of the survey period (Royle et al. 2004). This can be reasonably assumed because my survey was conducted during the peak of the grassland bird breeding season, when birds are relatively stationary, because they are defending established territories. Additionally, because each year was analyzed separately, associations seen in 2014 should be independent of those in 2015. It has been suggested that violation of closure will be apparent in lack of model fit (Thompson et al. 2014), when tested by parametric bootstrapping in 'unmarked' (Royle et al. 2004). Parametric bootstrapping simulates new bird abundance data by using the estimated parameters of the model. The model's goodness-of-fit (GOF) was tested by comparing the chi-squared statistic of the real data to the distribution of the chi-squared statistics generated from multiple runs of simulated data through the model (Kéry and Royle

2016).The data from the two years were analyzed separately, because vegetation survey methods differed slightly between years.

Model Selection

A multi-step selection process similar to that employed by Thompson et al. (2014) was used determine the best model for both detection and abundance covariates. This process involves model selection in three steps. The first step is determining which detection covariates (e.g. time of day) influence detection probability for each bird species. This is done prior to the vegetation selection process because considering the effects of vegetation on bird abundance without accounting for detection could result in false conclusions (Thompson et al. 2014). The second step in model selection was to choose only one of three correlated measures of vegetation structure, VOR, live vegetation height, and litter depth. This vegetation structure model selection process included the best model of detection. The third step in model selection incorporated the best detection model, the best measure of vegetation structure, and three additional measures of vegetation: bare ground, percent of grass, count of woody plants. This third and final model was then reduced to the most parsimonious measures of vegetation that explain bird abundance.

For all model selection steps I used Akaike's Information Criterion (AIC) to select the top model (Burnham and Anderson 2002). I did not use AIC corrected for small sample size because it is unclear what the effective sample size is for *N*-mixture modeling (Kéry and Royle 2016). If the top model was not separated from other

competing models by >2 AIC units, I chose the model with the lowest number of covariates and lowest AIC. Both detection and vegetation covariates were standardized by subtracting each covariate value from the group mean and dividing by the group standard deviation, to maximize model convergence and simplify interpretation (Zuur et al. 2009).

Detection Model

The following were included as detection covariates: hours after sunrise, day of the season, and wind speed. All additive combinations of detection covariates were considered as models (e.g., time+date+wind, time+wind, time+date…). Interactions were not considered due to limited sample size. All candidate detection models included the same four vegetation covariates: VOR, bare ground, count of woody plants, and percent grass coverage. Candidate detection models were only fitted with a Poisson mixture. Vegetation covariates were included in the detection selection procedure because comparing detection covariates without any vegetation covariates could result in spurious conclusions (Thompson et al. 2014).

Vegetation Structure Model

After selection of detection covariates I created 14 models to assess the influence of local vegetation structure and structural variation on bird abundance (Table 19). I included mean and SD of visual obstruction reading (VOR), litter depth, and vegetation height for each bird point to test if mean vegetation structure or variation in structure influence bird abundance. Each model only included a single type

of vegetation measure. Quadratic and linear terms were included, since plots of raw abundance showed a peak in bird abundance. Quadratic terms were not included without the corresponding linear term. The vegetation covariate from the most parsimonious vegetation structure model was included in the final habitat model.

Final Habitat Model

The final habitat model (FHM) selection combined the top detection covariates and the top vegetation structure covariates selected in the previous steps, with additional measures of vegetation. I included percent grass coverage, percent bare ground, and count of all woody plants. These measures were included in 10 models (Table 11) based on prior knowledge of vegetation characteristics that are important to grassland birds (Thompson et al. 2014, Fisher and Davis 2010). The top model was selected using AIC rank. If the null or detection only model was included in the list of top models, no vegetation covariates were considered to be reasonable predictors of abundance. I assessed the goodness-of-fit of the most parsimonious FHM for each species by comparing the Pearson's chi-square statistic of the observed data to a distribution of chi-square statistics generated by parametric bootstrapping (MacKenzie and Bailey 2004). A model was considered to have adequate fit if the p-value from the chi-square statistic for observed data when compared to the simulated data was >0.05. I simulated 1000 datasets to test GOF using the 'Nmix.gof.test' function from the 'AICcmodavg' package (Mazerolle 2016). In the interest of clarity I averaged the beta coefficients for bird species that had multiple top models using the package 'AICcmodavg' (Mazerolle 2016).

I used the best FHM for each species to generate predictions of abundance across the entire range of observed vegetation values present in the model. When the best model contained multiple covariates all other terms were held at their mean values while the term of interest was allowed to vary across the range of measured covariate values.

Prescribed Burning Analysis

I compared the estimated densities of focal bird species when accounting for detection, between burned and unburned units in the pre-fire year (2014), and the post-fire year (2015) by adding in a model term for burning treatment. If a bird species showed a significant change in abundance after burning I then tested if the effect of burning treatment was still significant when controlling for vegetation structure. I controlled for vegetation by adding in vegetation covariates from each competing FHM. The effect of burning was considered significant if the 95% CI of the beta coefficient for burning treatment did not overlap zero. For instance, if the top FHM for Western Meadowlark had time of day as the detection covariate and VOR as the vegetation covariate, the model testing the effect of burning while controlling for vegetation would have VOR and burning treatment as vegetation covariates. If a species had multiple top FHMs, each had the term for burning treatment added along with all vegetation covariates for that FHM. My main goal was determining which vegetation measure best explained the change in bird abundance after burning. Presumably the vegetation covariates present in the top FHMs are strongly correlated with bird territory selection.

Results

Live vegetation height and litter depth were lower in burned units compared to unburned units (Table 12). Live vegetation height and VOR were positively correlated between years across all units, and within unburned and burned units (Table 13). Litter depth was not correlated between years, indicating greater seasonal variation in litter (Table 13). VOR and live vegetation height from both years were significantly correlated, but VOR was not significantly correlated with litter depth in 2014 or 2015 (Table 13). The relationship between litter depth and VOR was essentially flat, with litter depth showing little variation across the entire range of measured VOR.

Out of all observed bird species, the most frequently detected grassland species in 2014 were Savannah Sparrow (27% of all detections, 276 total detections), Clay-colored Sparrow (18% and 181), Sedge Wren (13% and 128), Bobolink (9% and 90), and Western Meadowlark (8% and 77). The most frequently detected grassland species in 2015 were Savannah Sparrow (27% and 365), Clay-colored Sparrow (17% and 226), Sedge Wren (15% and 202), Bobolink (6% and 84), and Western Meadowlark (6% and 78). Species richness across the entire site increased from 23 bird species prior to burning, to 31 the year after prescribed burning. Three bird species detected during the pre-fire year were not detected in the post-fire year: Wilson's Phalarope (*Phalaropus tricolor*), Yellow Rail (*Coturnicops noveboracensis*), and Yellow Warbler (*Setophaga petechia*). Thirteen new species were detected during the post-fire year: American Robin (*Turdus migratorius*), Brewer's Blackbird (*Euphagus cyanocephalus*), Brown Thrasher (*Toxostoma rufum*), Cedar Waxwing (*Bombycilla cedrorum*), Eastern Kingbird

(*Tyrannus tyrannus*), Gray Catbird (*Dumetella carolinensis*), Killdeer (*Charadrius vociferus*), Marbled Godwit (*Limosa fedoa*), Mallard (*Anas platyrhynchos*), Mourning Dove (*Zenaida macroura*), Northern Flicker (*Colaptes auratus*), Swamp Sparrow (*Melospiza georgiana*), and Upland Sandpiper (*Bartramia longicauda*).

All bird species had at least one detection covariate selected for inclusion in the top detection model in at least one year. There were a variety of covariates that explained detection probability for each bird species (Table 14), with the number of competing detection models ranging from three to five. In both years Bobolink detection probability declined with day of season (Table 15). In 2014 Clay-colored Sparrow detection probability weakly increased with day of season (β= 0.16±0.10), and was not influenced by any covariates in 2014 (Table 15). Savannah Sparrow detection probability was not influenced by any covariates in 2014 and increased with day of season in 2015 (Table 16). Sedge Wren detection probability declined with time of day in both 2014 and 2015, and increased with day of season in 2015 (Table 16). Western Meadowlark detection probability declined weakly with time of day (β= -0.24±0.13) in 2014 and day of season (β= -0.20±0.12) in 2015 (Table 17).

The majority of bird species had at least two competing vegetation structure models in 2014 and 2015. Either VOR or VOR^2 was selected as the most parsimonious model for 4 of 5 species in 2014, and 2 of 5 species in 2015. The most parsimonious Bobolink vegetation structure model was VOR in 2014 and litter $depth^2$ in 2015 (Table 18). The most parsimonious Clay-colored Sparrow vegetation structure model included VOR in both years (Table 18). The most parsimonious Savannah Sparrow vegetation

structure model was VOR in 2014 and detection in 2015 (Table 18). The most parsimonious Sedge Wren vegetation structure model was VOR in 2014 and litter depth in 2015. The most parsimonious Western Meadowlark vegetation structure model was live vegetation height in 2014 and VOR in 2015.

Top FHMs for each of the five species showed adequate fit after testing goodness-of-fit using parametric bootstrapping for Bobolink (2014: p=0.550, ĉ=0.96; 2015: p=0.626, ĉ=1), Clay-colored Sparrow (2014: p=0.995, ĉ=0.70; 2015: p=0.709, ĉ=0.91), Savannah Sparrow (2014: p=1.000, ĉ=0.61; 2015: p=1.000,ĉ=0.52), Sedge Wren (2014: p=0.923, ĉ=0.79; 2015: p=0.999, ĉ=0.64), and Western Meadowlark (2014: p=0.970, ĉ=0.78, 2015: p=1.000, ĉ=0.67). Although some species showed signs of underdispersion (ĉ<1.0), a sign of lower variation in bird abundance than would be expected, this can be ignored at this risk of overinflating error (Kéry and Royle 2016). I used top FHMs in all subsequent analyses, because I would rather exercise caution when testing changes for changes in abundance due to treatment. The application of a management treatment can have lasting effects on wildlife communities, so it is better to err on the side of caution when interpreting effects.

For the top FHMs the strongest effects came from measures of vegetation selected in the vegetation structure model process. The top FHM changed little for species that showed no change in abundance between burned and unburned units in 2015 (Table 19). In both years Clay-colored Sparrows were positively associated with amount of woody vegetation (Table 15). All other species had variable responses to woody vegetation between years. For instance Bobolink showed a weak negative

response to woody vegetation (β= -0.06±0.16) in the year prior to burning and strong negative response (β= -0.45±0.19) the year after burning. While coverage of grass and bare ground were included in the list of top FHMs (Table 19) they did not significantly affect the abundance of any species. It is also notable that amount of woody vegetation, bare ground, and grass coverage were rarely included in the list of top FHMs without VOR, litter depth, or live vegetation height (Table 19).

Three of the five bird species showed a significant difference in abundance after prescribed burning (Table 11). Bobolink abundance was 3.8 times lower in burned units versus unburned units (Figure 16). Sedge Wren abundance was 2.2 times lower in burned units versus unburned units (Figure 16). Western Meadowlark abundance was 1.9 times higher in burned units versus unburned units (Figure 17). Clay-colored Sparrow (Figure 17), Savannah Sparrow (Figure 18) had no significant change in abundance after prescribed burning. When the top FHMs for Bobolink (Figure 19), Sedge Wren (Figure 20), and Western Meadowlark (Figure 21) had burn treatment term incorporated, the effect of burning was no longer found to be significant. This suggests that changes in the most important measures of vegetation, covariates in the top FHM, are contributing the most to differences in bird abundance.

Discussion

Prescribed burning affected Bobolink, Sedge Wren and Western Meadowlark abundance. The abundance of species that prefer denser vegetation, Bobolink and Sedge Wren (Thompson et al. 2014), declined in units that were burned, while Western Meadowlark which are associated with sparser vegetation (Madden et al. 2000), increased in abundance. This change in bird abundance is in response to change in vegetation structure, most likely lower litter depth and to a lesser extent lower vegetation height in burned units. It appears that Bobolink and Sedge Wren use early season indicators of vegetation structure such as litter depth to make settlement decisions when an area is disturbed. Although it is also possible that density of dead vegetation prior to the growing season was used by birds as an indicator of future habitat structure. Low intensity fall burning of Oakville did little to reduce amount of woody plants present, one possible reason for the lack of change in Clay-colored Sparrow abundance.

Few studies have incorporated detection probability when examining the response of grassland birds to prescribed burning (e.g. Rahmig et al. 2009), and the majority have not (e.g. Robel et al. 1998, Grant et al. 2010). Without accounting for the additional variation produced by varying detection rates, researchers are more likely to commit Type I errors making their inferences suspect. One study found that when considering changes in bird species richness in California over 100 years, when detection was not accounted for bird richness increased over that time period, but when detection was incorporated the opposite was true, richness declined (Tingley and

Beissenger 2013). With detection probability controlled for in my study I am able to make more accurate inferences about changes in bird abundance relative to the application of fire.

The shift from VOR to litter depth as the best vegetation structure model for Bobolink and Sedge Wren is logical given that there was little change in VOR after burning (Table 16). The strength of the relationship between bird abundance and litter depth after burning suggest that either litter depth or density of dormant vegetation prior to the start of the growing season are what Bobolink and Sedge Wren use as predictors of future vegetation structure. Dead vegetation density has been shown to have a significant effect on grassland bird habitat use in mixed-grass prairie (Davis 2005). Litter depth is usually highly correlated with VOR, but in the year prior to burning there was no significant relationship. This lack of correlation may be due to the absence of disturbance for >30 years on Oakville, allowing litter to accumulate evenly across the site. If birds use litter depth after disturbance as a cue for future habitat quality they may be abandoning burned areas unnecessarily, when in fact these areas had little change in VOR. The use of litter depth as an indicator of future habitat quality makes sense in light of the historical disturbance regime of burning followed by grazing in the Great Plains (Knapp et al. 1999). Bison preferentially graze recently burned areas, resulting in patches of sparse vegetation and low litter where they graze, with vegetation density increasing with time since grazing (Fuhlendorf and Engle 2004). The relationship between low litter and low vegetation density should hold in a burned and grazed system, but would not in a system that has grazers absent.

My results lend support to the importance of litter depth for habitat settlement decisions, which many previous studies did not give an explicit justification for including in model selection (Fisher and Davis 2010). Winter suggested that litter is important for use in nest building (2005a). While this study is not able to provide the mechanism driving selection of a specific litter depth, it can point to its importance. When litter depth was reduced without a proportional change in VOR in my study, litter depth became the best predictor of abundance for two species, suggesting that it may play a more important role apart from VOR. There has been little evidence of a link between greater litter depth and increased nest survival for grassland species (Davis 2005). It has been suggested that the lack of a fitness advantage for birds nesting in denser vegetation could be due to the variety of predators present in a grassland (Dion et al. 2000), with nests in both sparse and dense vegetation threatened by predation.

An alternative explanation may be that birds are using areas that balance efficient foraging with predation risk. Western Meadowlark, like other icterids, uses gaping (opening of the bill in soil), to probe for insects (Beecher 1951) and may have been opportunistically using recently burned areas for foraging since prey would be more visible. In the UK, European Starlings (*Sturnus vulgaris*) foraging efficiency was 33.2% greater in short grassland than in denser grassland areas, presumably due to better visibility of prey (Devereux et al. 2004). Meadowlarks are also larger bodied species with a wing-chord of 127.0 ± 3.0 SE (Davis and Lanyon 2008) relative to Sedge Wren and Bobolink, with wing-chords of 44.03 mm ± 0.21 SE (Herkert et al. 2001) and 97.4 mm ± 2.8 SE (Bollinger and Gavin 1989) respectively. It is logical Western

Meadowlark would not be able to navigate dense vegetation as well as other smaller bodied species. Even though predation risk may be lower in denser vegetation, foraging efficiency may limit its benefit.

In mixed-grass prairie Western Meadowlark nests were associated with tall dense vegetation (Davis 2005), while my results appear to contradict this I was only able to make generalizations about habitat that is used over a large area. Additionally vegetation density is a relative term, so tall and dense in mixed-grass prairie could be intermediate density of vegetation in tallgrass prairie. Western Meadowlarks may have been nesting in denser portions of burned units, but my data collection was not fine scale enough to discern that level of habitat use. Another study in mixed-grass prairie found that Western Meadowlarks prefer sparser shorter vegetation and more litter (Madden et al. 2000). These two studies highlight the variability in habitat preference even within the same ecoregion and may suggest that in the northern tallgrass prairie Western Meadowlarks have a preference for more open habitat. A study in northern mixed-grass prairie tested the effect of burning on grassland birds found no significant change in Western Meadowlark abundance with time since fire (Grant et al. 2010), lending further supporting a possible regional difference in habitat preference. It is difficult to make sweeping generalizations based on the results of my study since it had no spatial and little temporal replication. The decline Bobolink densities after fire is supported by research from mixed-grass prairie (Grant et al. 2010), as is the decline in Sedge Wren abundance by research conducted in tallgrass prairie (Robel et al. 1998). The preference of Bobolink and Sedge Wren for denser vegetation is well documented

for both mixed-grass (Madden et al. 2000) and tallgrass prairie (Winter et al. 2005a, Thompson et al. 2014, Ahlering and Merkord 2016). Based on our results it appears there is less variation in habitat preference and response to fire from Sedge Wren and Bobolink between regions.

While prescribed burning had a negative effect on two of five grassland bird species that were considered in this study, burning did generate a mosaic of vegetation across the site that was beneficial to many more bird species than we are able to model due to their low abundances. This benefit to birds is supported by the increase in bird richness across the site the year after burning. Of the new species detected on the site after prescribed burning, Killdeer and Upland Sandpiper may have benefited from the more open habitat generated by burning because they are known to use row crop fields in addition to shore habitat (Rottenborn 1996). The results from this study also suggest that managers may have to use forms of management other than fall burning, or more frequent application of burning, if their goal is to decrease vegetation density and abundance of woody vegetation. Few studies have demonstrated a strong relationship between litter depth and bird abundance when VOR is uncorrelated to litter (but see Ahlering and Merkord 2016). My results suggest that at least for Bobolink and Sedge Wren, litter depth could be an important vegetation metric for managers. For instance, the choice of whether to collect cut vegetation after haying could have an influence on bird use of an area, regardless of difference in vegetation density. With a better understanding of how grassland species respond to prescribed burning throughout the tallgrass prairie and across the northern Great Plains, managers target specific types of

vegetation structure for management and may have to use a variety of management techniques to give the most benefit to multiple grassland bird species.

Literature Cited

Ahlering, M. A., and C. L. Merkord. 2016. Cattle grazing and grassland birds in the northern tallgrass prairie. Journal of Wildlife Management 80:Early View Online.

Bakker, K., D. Naugle, and K. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Beecher, W. J. 1951. Adaptation for food-getting in the American blackbirds. Auk 68:411–440.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird census techniques. Second Edition. Academic Press, London, UK.

Bollinger, E., and T. Gavin. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. Auk 106:584–594.

Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds : an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media. New York, USA.

Coppedge, B. R., S. D. Fuhlendorf, W. C. Harrell, and D. M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. Biological Conservation 141:1196–1203.

Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107:605.

Devereux, C. L., C. U. Mckeever, T. G. Benton, and M. J. Whittingham. 2004. The effect of sward height and drainage on common starlings (Sturnus vulgaris) and northern lapwings (Vanellus vanellus) foraging in grassland habitats. Ibis 146:115–122.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12:53–64.

Dion, N., K. a Hobson, and S. Larivière. 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. Condor 102:629–634.

Dyke, S. R., S. K. Johnson, and P. T. Isakson. 2015. North Dakota State Wildlife Action Plan. North Dakota Game and Fish Department. Bismarck, ND.

Fisher, R., and S. Davis. 2010. From Wiens to Robel: a review of grassland bird habitat selection. Journal of Wildlife Management 74:265–273.

Fiske, I., and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Fuhlendorf, S., W. Harrell, D. Engle, R. Hamilton, C. Davis, and D. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706-1716.

Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598.

Grant, T. A, E. M. Madden, T. L. Shaffer, and J. S. Dockens. 2010. Effects of Prescribed Fire on Vegetation and Passerine Birds in Northern Mixed-Grass Prairie. Journal of Wildlife Management 74:1841–1851.

Grant, T. A., T. L. Shaffer, E. M. Madden, and G. B. Berkey. 2011. Ducks and passerines nesting in northern mixed-grass prairie treated with fire. Wildlife Society Bulletin 35:368-376.

Hovick, T. J., J. R. Miller, S. J. Dinsmore, D. M. Engle, D. M. Debinski, and S. D. Fuhlendorf. 2012. Effects of fire and grazing on grasshopper sparrow nest survival. Journal of Wildlife Management 76:19–27.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5:1-13.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications 25:662–672.

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. Applied Hierarchical Modeling in Ecology. First edition. Elsevier, London, UK.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39.

Lauenroth, W. K., I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Research 9:223–259.

Long, A. M., W. E. Jensen, and R. S. Matlack. 2014. Influence of prescribed burning on bird abundance and species assemblage in a semiarid Great Plains grassland. Western North American Naturalist 74:396–404.

MacKenzie, D., and L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

Madden, E., and R. Murphy. 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144:377–392.

Mazerolle, M. J. 2016. AICcmodavg: model selection and multimodel inference based on (Q)AICc. R package version 2.0-4. http://CRAN.R-project.org/package=AICcmodavg. Accessed 1 April 2016.

Rahmig, C. J., W. E. Jensen, and K. A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. Conservation Biology 23:420–32.

Robel, R. J., J. P. Hughes, S. D. Hull, K. E. Kemp, and D. S. Klute. 1998. Spring Burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management 51:132–138.

Rollfinke, B. F., and R. H. Yahner. 1990. Effects of time of day and season on winter bird counts. Condor 92:215–219.

Rottenborn, S. C. 1996. The use of coastal agricultural fields in Virginia as foraging habitat by shorebirds. Wilson Bulletin 108:783–796.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Sauer, J., W. Link, and J. Fallon. 2013. The North American breeding bird survey 1966-2011: summary analysis and species accounts. North American Fauna 79:1–32.

Thompson, S. J., T. W. Arnold, and C. L. Amundson. 2014. A multiscale assessment of tree avoidance by prairie birds. Condor 116:303–315.

Tingley, M. W., and S. R. Beissinger. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. Ecology 94:598–609.

Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland nesting birds. Conservation Biology 13:1424–1436.

Winter, M., and D. Johnson. 2004. Nesting biology of three grassland passerines in the northern tallgrass prairie. Wilson Bulletin 116:211–223.

Winter, M., D. Johnson, J. Shaffer, M. Therese, and D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70:158–172.

Winter, M., D. H. Johnson, J. Shaffer, and A. n.d. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

Wright, C., and M. Wimberly. 2013. Recent land use change in the western corn belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences 110:4134–4139.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag. New York, USA.

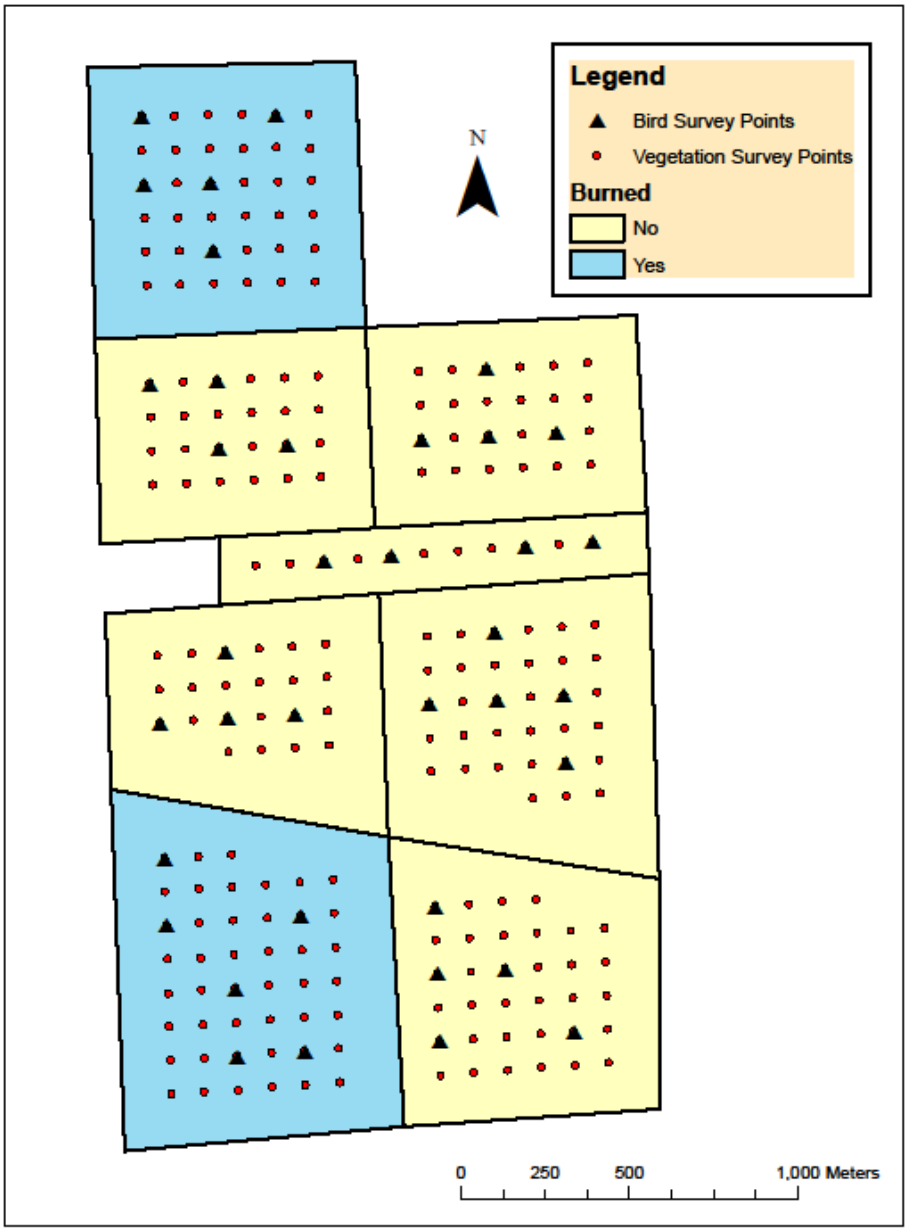

Figure 14. Map of Oakville Prairie Field Station sampling locations. Management unit boundaries are represented by bold black outlines. Colors denote burning treatment.

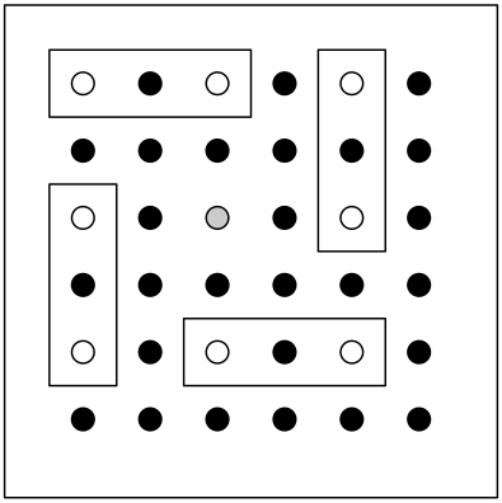

Figure 15. Example of a typical management unit at Oakville. The management unit boundary is represented by the large black square. All points are established vegetation survey locations. Hollow points are potential bird point count locations. Grey point is the central bird point. Small rectangles are sections of the unit.

Table 10. Description of all candidate models for the vegetation structure model selection process. VOR=visual obstruction reading (cm), LIVEHT=live vegetation height (cm), LIT=litter depth (cm), SD=standard deviation, DATE=day of season, TIME=time of day, WIND=wind speed (Beaufort scale).

Model	Covariates
Null	None
Det	Best model from detection covariate selection (DATE, TIME, WIND)
3	Det + VOR
4	Det + VOR + VOR^2
5	Det + VORSD
6	Det + VORSD + $VORSD^2$
7	Det + LIVEHT
8	Det + LIVEHT + $LIVEHT^2$
9	Det + LIVEHTSD
10	Det + LIVEHTSD + $LIVEHTSD^2$
11	Det + LIT
12	Det + LIT + LIT^2
13	Det + LITSD
14	Det + LITSD + $LITSD^2$

Table 11. Description of all candidate models for the final habitat model selection process. DATE=day of season, TIME=hours after sunrise, WIND=wind speed (Beaufort scale), VOR=visual obstruction reading (cm), LIVEHT=live vegetation height (cm), LIT=litter depth (cm), BARE=percent bare ground, GRASS=percent grass coverage, WOODY=sum of trees and shrubs, SD=standard deviation.

Model Name	Covariates
Null	None
Detection	Best model from detection covariate selection (DATE, TIME, WIND)
Structure	Detection + Best model from vegetation structure model selection (VOR, LIT, LIVEHT, or SD)
Bare	Detection + BARE
Grass	Detection + GRASS
Woody	Detection + WOODY
Structure + Bare	Detection + Structure + BARE
Structure + Grass	Detection + Structure + GRASS
Structure + Woody	Detection + Structure + WOODY
Full	Detection + Structure + BARE + GRASS + WOODY

Table 12. Comparison of change in vegetation structure from 2014 to 2015 in burned and unburned units. Negative numbers represent a mean decline in a vegetation measure from 2014 to 2015. Change in structure was compared using a Welch's t-test. Vegetation that showed a significant difference between treatments is bolded.

	Treatment				
Vegetation	Unburned	Burned	t	df	p
LIVE	**12.56 cm**	**3.99 cm**	2.20	14.75	<0.05
LIT	**2.29 cm**	**-2.33 cm**	7.98	18.86	<0.0001
VOR	9.17 cm	5.80 cm	1.04	14.32	0.3137
FORB	-8.2 %	0.6 %	-1.38	16.92	0.1849
GRASS	10.8 %	2.6 %	1.18	15.77	0.2563
BARE	-0.4 %	2.9 %	-1.94	10.40	0.0797
WOODY	-3.3	-11.8	1.80	16.77	0.0908

Table 13. Pearson's correlation coefficients between measures of vegetation structure in 2014 and 2015. The number before a vegetation term denotes the year that it was collected. Both- correlation for all points (n=37), Unburned- correlation for points in unburned units (n=26), Burned- correlation for points in burned units (n=11). ***- p<0.0001, **- p<0.01, * p<0.05

	Treatment		
Comparison	Both	Unburned	Burned
14 VOR & 14 LIVEHT	0.88***	0.88***	0.94***
15 VOR & 15 LIVEHT	0.94***	0.85***	0.98***
14 VOR & 14 LIT	0.10	-0.17	0.51
15 VOR & 15 LIT	0.39*	0.29	0.51
14 LIVEHT & 14 LIT	0.32	-0.10	0.70*
15 LIVEHT & 15 LIT	0.39*	0.22	0.49
14 VOR & 15 VOR	0.76***	0.71***	0.83**
14 LIVEHT & 15 LIVEHT	0.61***	0.55**	0.75**
14 LIT & 15 LIT	-0.32	-0.17	0.02

Table 14. Top models from the detection model selection process. List of models was truncated at 2 ΔAIC for clarity. Models that were selected as most parsimonious are bolded and k is the number of model parameters. DATE- day of season, TIME- hours after sunrise, WIND- Beaufort scale wind speed.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	**7**	**DATE**	**0.00**	**7**	**DATE**	**0.00**
	8	TIME+DATE	1.85	8	TIME+DATE	1.36
	8	DATE+WIND	2.00	8	DATE+WIND	1.91
Clay-colored Sparrow	8	DATE+WIND	0.00	7	WIND	0.00
	8	TIME+DATE	1.22	**6**	**NULL**	**0.69**
	7	**DATE**	**1.25**	7	TIME	1.09
	9	ALL	1.46	8	TIME+WIND	1.68
	-	-	-	8	DATE+WIND	1.98
Savannah Sparrow	7	DATE	0.00	8	TIME+DATE	0.00
	8	DATE+WIND	1.72	**7**	**DATE**	**0.73**
	8	TIME+DATE	1.78	8	DATE+WIND	1.23
	6	**NULL**	**1.97**	9	ALL	1.89
Sedge Wren	**7**	**TIME**	**0.00**	9	ALL	0.00
	8	TIME+WIND	1.67	**8**	**TIME+DATE**	**0.56**
	8	TIME+DATE	1.89	8	DATE+WIND	1.94
Western Meadowlark	8	DATE+WIND	0.00	**7**	**DATE**	**0.00**
	8	TIME+DATE	0.67	8	DATE+WIND	0.79
	9	FULL	1.27	6	NULL	0.89
	7	**TIME**	**1.45**	8	TIME+DATE	1.82
	7	DATE	1.61	-	-	-

Table 15. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Bobolink and Clay-colored Sparrow for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate a zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Abundance covariates are defined in Table 11.

	Bobolink				Clay-colored Sparrow			
	2014		2015		2014		2015	
	β	SE	β	SE	β	SE	β	SE
Detection								
Intercept (p)	-3.30	3.53	-1.61	0.66	-1.05	0.83	0.23	0.23
DATE (p)	**-0.69**	0.16	**-0.52**	0.14	0.16	0.10	-	-
TIME (p)	-	-	-	-	-	-	-	-
WIND (p)	-	-	-	-	-	-	**-**	-
Abundance								
Intercept (λ)	3.25	3.39	1.35	0.64	2.00	0.61	0.91	0.14
VOR (λ)	**-0.48**	0.16	**-**	-	0.06	0.16	**0.23**	0.14
VOR^2 (λ)	**-0.47**	0.16	**-**	-	**-0.38**	0.15	-	-
LIVEHT (λ)	-	-	-	-	-	-	-	-
$LIVEHT^2$ (λ)	-	-	-	-	-	-	-	-
LIT (λ)	-	-	0.45	0.24	-	-	-	-
LIT^2 (λ)	-	-	**-0.65**	**0.24**	-	-	-	-
WOODY (λ)	-0.06	0.16	**-0.45**	**0.19**	**0.34**	0.12	**0.25**	0.10
GRASS (λ)	0.01	0.13	-1.44	1.35	-0.27	0.10	-0.19	0.12
BARE (λ)	-0.10	0.13	-0.21	0.18	-0.01	0.09	-0.39	0.30

Table 16. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Savannah Sparrow and Sedge Wren for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate a zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Abundance covariates are defined in Table 11.

	Savannah Sparrow				Sedge Wren			
	2014		2015		2014		2015	
	β	SE	β	SE	β	SE	β	SE
Detection								
Intercept (p)	-2.82	0.54	0.20	0.26	-0.10	0.32	-0.09	0.30
DATE (p)	**-**	-	**0.29**	0.09	-	-	**0.27**	0.11
TIME (p)	-	-	-	-	**-0.65**	0.17	**-0.34**	0.12
WIND (p)	-	-	-	-	-	-	**-**	-
Abundance								
Intercept (λ)	3.70	0.51	1.48	0.13	0.77	0.19	1.05	0.19
VOR (λ)	**-0.31**	0.09	**-**	-	**0.35**	0.15	**-**	-
VOR^2 (λ)	**-**	-	**-**	-	**-**	-	-	-
LIVEHT (λ)	-	-	-	-	-	-	-	-
$LIVEHT^2$ (λ)	-	-	-	-	-	-	-	-
LITTER (λ)	-	-	-	-	-	-	**0.48**	0.14
$LITTER^2$ (λ)	-	-	**-**	**-**	-	-	-0.11	0.11
WOODY (λ)	-0.14	0.09	**-0.23**	0.10	**-**	-	0.00	0.11
GRASS (λ)	0.17	0.09	-	-	-0.24	0.14	-0.06	0.12
BARE (λ)	-0.05	0.08	-	-	-	-	-0.39	0.30

Table 17. Estimates of beta coefficients for detection covariates (p), and abundance covariates (λ) for Western Meadowlark for 2014 and 2015. Beta coefficients were averaged across all competing final habitat models. If a competing model was missing a covariate a zero was not added to the average. All beta coefficients that have 95% confidence intervals that do not overlap zero are bolded. Abundance covariates are defined in Table 11.

	Western Meadowlark			
	2014		2015	
	β	SE	β	SE
Detection				
Intercept (p)	-2.43	1.99	-3.57	2.77
DATE (p)	**-**	-	**-0.20**	0.12
TIME (p)	-0.24	0.13	-	-
WIND (p)	-	-	-	-
Abundance				
Intercept (λ)	2.04	1.82	2.82	2.67
VOR (λ)	**-**	-	**-0.41**	0.13
VOR^2 (λ)	**-**	-	**-**	-
LIVEHT (λ)	-0.11	0.15	-	-
$LIVEHT^2$ (λ)	-	-	-	-
LITTER (λ)	-	-	-	-
$LITTER^2$ (λ)	**-**	**-**	-	-
WOODY (λ)	**-0.42**	**0.16**	-0.31	0.18
GRASS (λ)	-0.15	0.13	-	-
BARE (λ)	-0.29	0.18	-	-

Table 18. Top models from the vegetation structure model selection process. List of models was truncated at <2 ΔAIC for clarity. Models that were selected as most parsimonious are bolded and k is the number of model parameters. VOR- visual obstruction reading (cm), LIT- litter depth (cm), LIVEHT- live vegetation height (cm). Any term that is squared also included a linear term in the model.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	**5**	**VOR²**	**0.00**	**7**	**LIT²**	**0.00**
	5	LIVEHT²	1.37	9	LITSD²	0.10
Clay-colored Sparrow	**5**	**VOR²**	**0.00**	4	VOR²	0.00
	-	-	-	4	LIVEHT²	0.92
	-	-	-	3	LIVEHT	0.99
	-	-	-	**3**	**VOR**	**1.19**
Savannah Sparrow	**3**	**VOR**	**0.00**	4	VOR	0.00
	4	VOR²	1.95	5	VOR²	1.20
	-	-	-	**3**	**DET**	**1.56**
	-	-	-	4	LIVEHT	1.86
Sedge Wren	**4**	**VOR**	**0.00**	**5**	**LIT**	**0.00**
	4	LIVEHT	1.13	6	LIT²	0.66
	5	VOR²	1.97	**-**	**-**	**-**
Western Meadowlark	**4**	**LIVEHT**	**0.00**	**3**	**VOR**	**0.00**
	4	VORSD	0.04	3	LIVEHT	1.74
	4	VOR	0.31	4	VOR²	1.81
	4	LITSD	1.07	-	-	-
	5	LIVEHT²	1.53	-	-	-
	5	VORSD²	1.90	-	-	-

Table 19. Top models from the final habitat model process. List of models was truncated at <2 ΔAIC for clarity. Models that were selected as most parsimonious are bolded and k is the number of model parameters. VOR- visual obstruction reading (cm), LIT- litter depth (cm), LIVEHT- live vegetation height (cm), BARE- bare ground coverage, GRASS- percent grass coverage, WOODY- sum of tree and shrub count. Any term that is squared also included a linear term in the model.

	2014			2015		
Species	k	Model	ΔAIC	k	Model	ΔAIC
Bobolink	5	VOR^2	0.00	8	FULL	0.00
	6	VOR^2+BARE	1.43	6	LIT^2+WOODY	0.62
	6	VOR^2+WOODY	1.83	-	-	-
	6	VOR^2+GRASS	2.00	-	-	-
Clay-colored Sparrow	8	FULL	0.00	4	VOR+WOODY	0.00
	-	-	-	6	FULL	0.22
	-	-	-	4	VOR+GRASS	2.04
Savannah Sparrow	4	VOR+GRASS	0.00	4	WOODY	0.00
	6	FULL	0.97	-	-	-
Sedge Wren	5	VOR+GRASS	0.00	5	LIT	0.00
	4	VOR	1.14	6	LIT+BARE	0.78
	-	-	-	6	LIT+GRASS	1.54
	-	-	-	6	LIT+WOODY	1.94
Western Meadowlark	4	WOODY	0.00	4	VOR+WOODY	0.00
	5	LIVEHT+WOODY	1.36	3	VOR	1.29
	7	FULL	1.52	-	-	-

Table 20. Log-scale beta coefficient estimates for bird response to burning treatment when accounting for detection probability. Bolded beta coefficients have 95% CI that do not overlap zero.

	Pre-Burn		Post-Burn	
Species	Burn (β)	SE	Burn (β)	SE
Bobolink	-0.17	0.27	**-1.32**	0.46
Clay-colored Sparrow	-0.14	0.23	-0.11	0.24
Savannah Sparrow	0.13	0.17	0.10	0.18
Sedge Wren	-0.02	0.27	**-0.87**	0.30
Western Meadowlark	-0.51	0.34	**0.67**	0.28

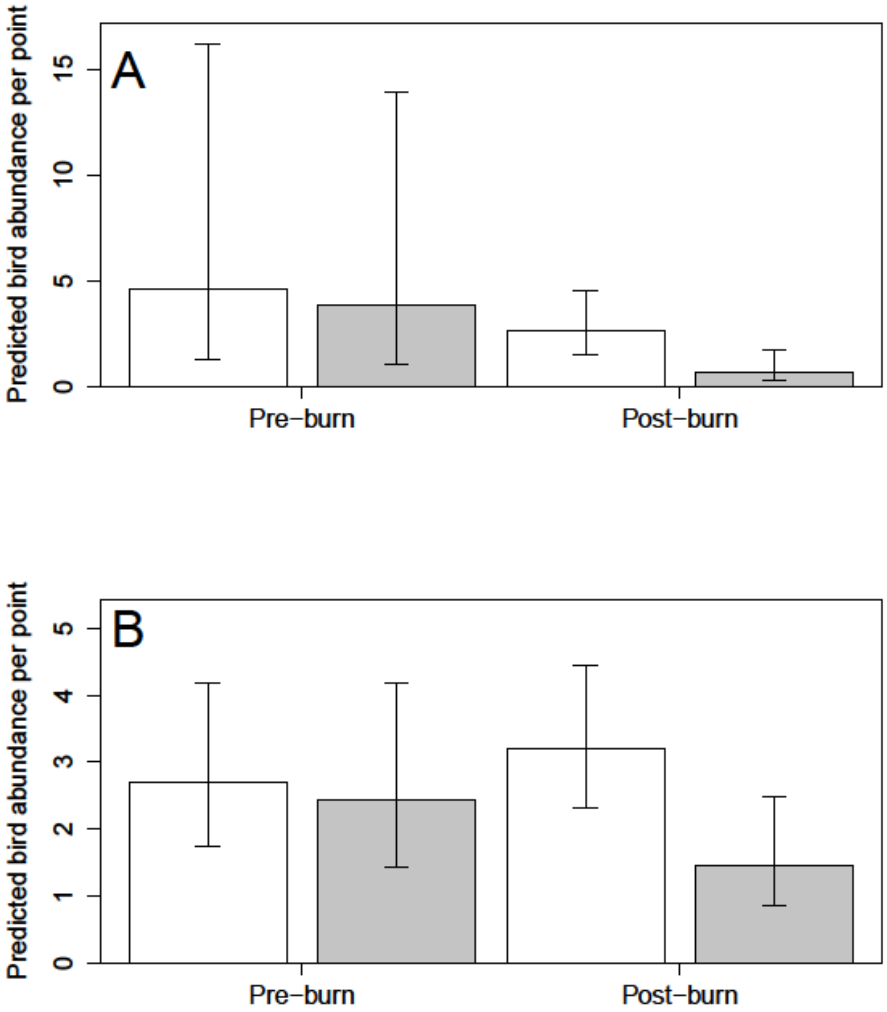

Figure 16. Mean predicted abundance of Bobolink (A) and Sedge Wren (B) pre-burn and post-burn seasons. Error bars represent 95% confidence intervals. White fill represents mean abundance in unburned units and grey fill burned units.

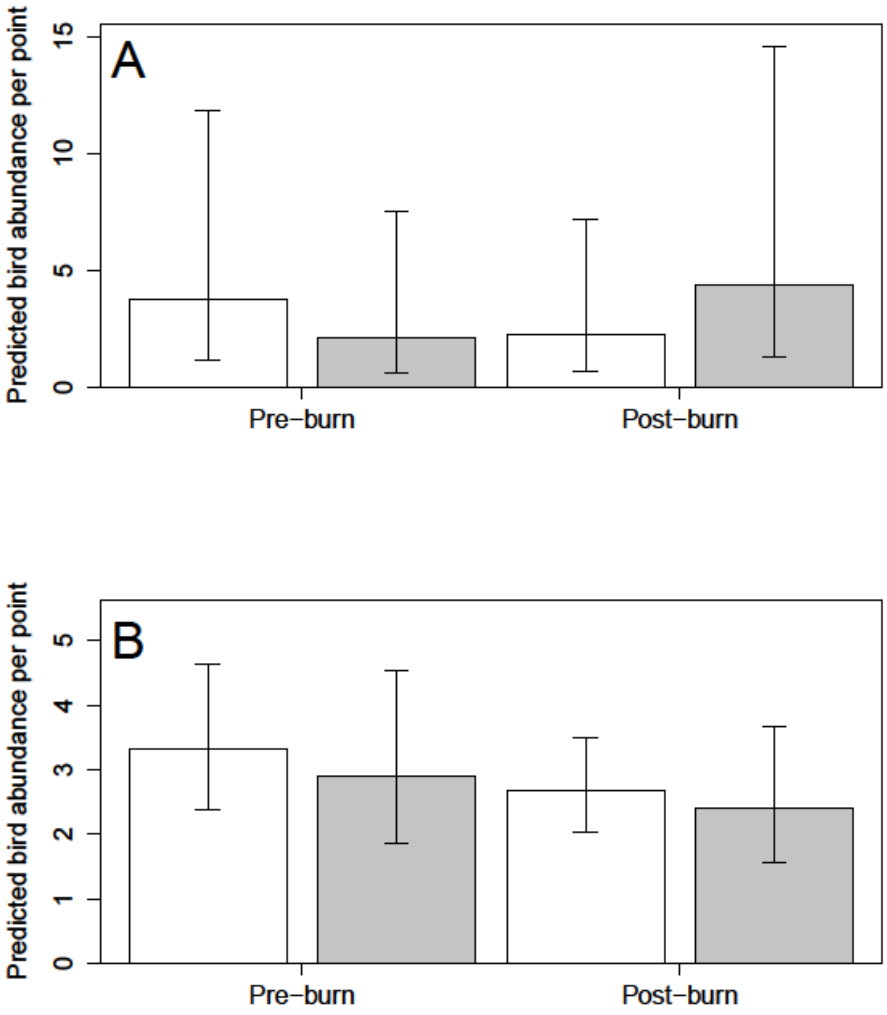

Figure 17. Mean predicted abundance of Western Meadowlark (A) and Clay-colored Sparrow (B) in pre-burn and post-burn seasons. Error bars represent 95% confidence intervals. White fill represents mean abundance in unburned units and grey fill burned units.

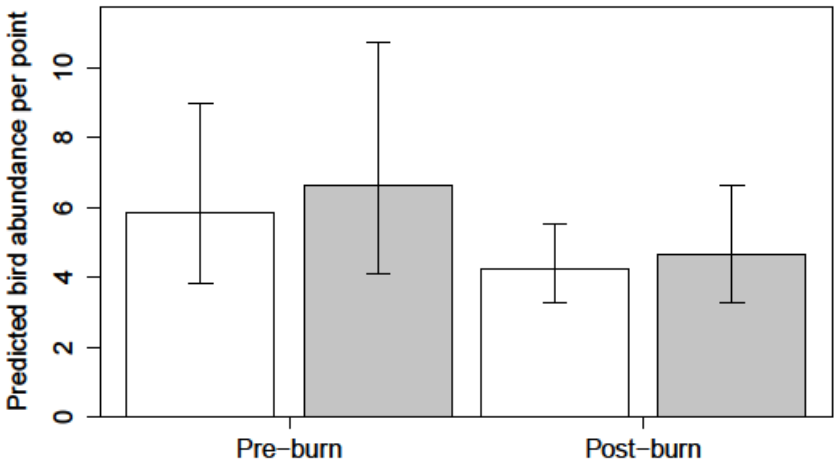

Figure 18. Mean predicted abundance of Savannah Sparrow in pre-burn and post-burn seasons. Error bars represent 95% confidence intervals. White fill represents mean abundance in unburned units and grey fill burned units.

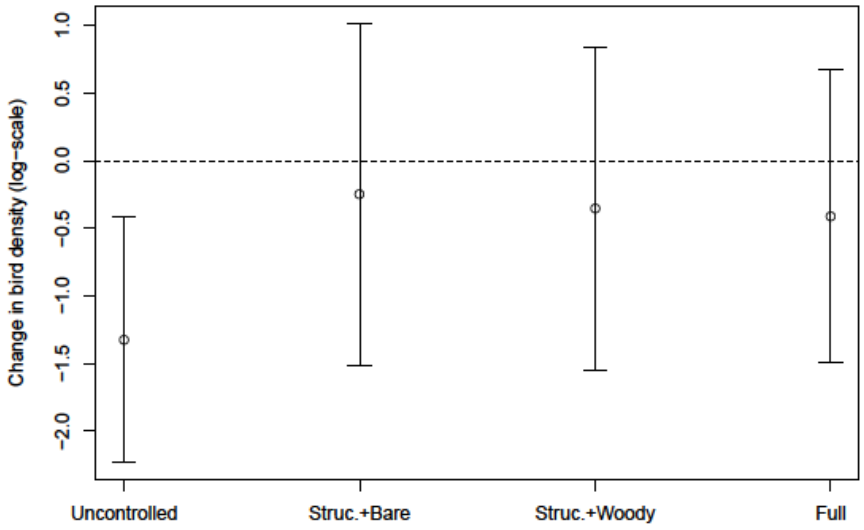

Figure 19. Difference in mean Bobolink abundance between unburned and burned treatments in 2015. Negative values represent lower bird abundance in burned units. Uncontrolled=difference in abundance accounting for detection probability only, Struc.+Bare= difference in abundance controlling for difference in vegetation structure and bare ground, Struc+Woody=difference in abundance controlling for difference in vegetation structure and count of woody plants, and Full=difference in abundance controlling for vegetation structure, count of woody plants, bare ground, and grass coverage. Error bars represent 95% confidence intervals.

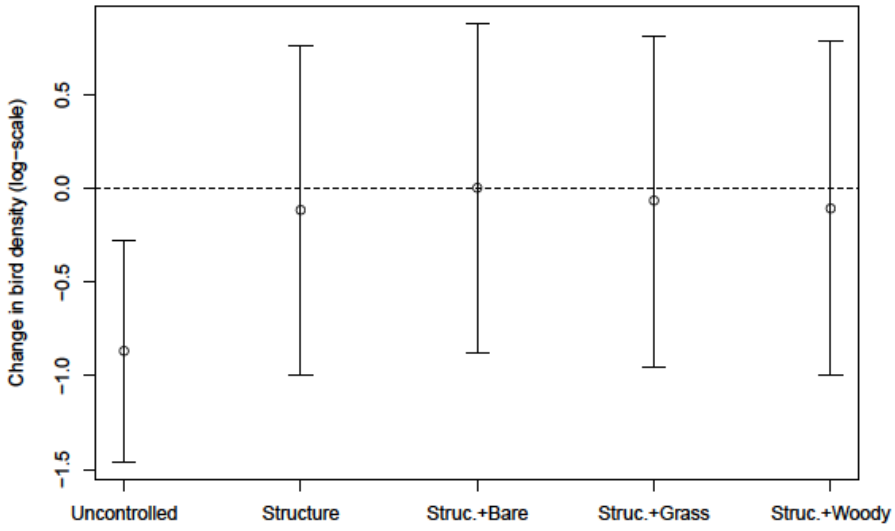

Figure 20. Difference in mean Sedge Wren abundance between unburned and burned treatments in 2015. Negative values represent lower bird abundance in burned units. Uncontrolled=difference in abundance accounting for detection probability only, Structure-difference in abundance controlling for vegetation structure, Struc.+Bare=difference in abundance controlling for difference in vegetation structure and bare ground, Struc+Grass=difference in abundance controlling for difference in grass coverage, Struc+Woody=difference in abundance controlling for difference in vegetation structure and count of woody plants, and Full- difference in abundance controlling for vegetation structure, count of woody plants, bare ground, and grass coverage. Error bars represent 95% confidence intervals.

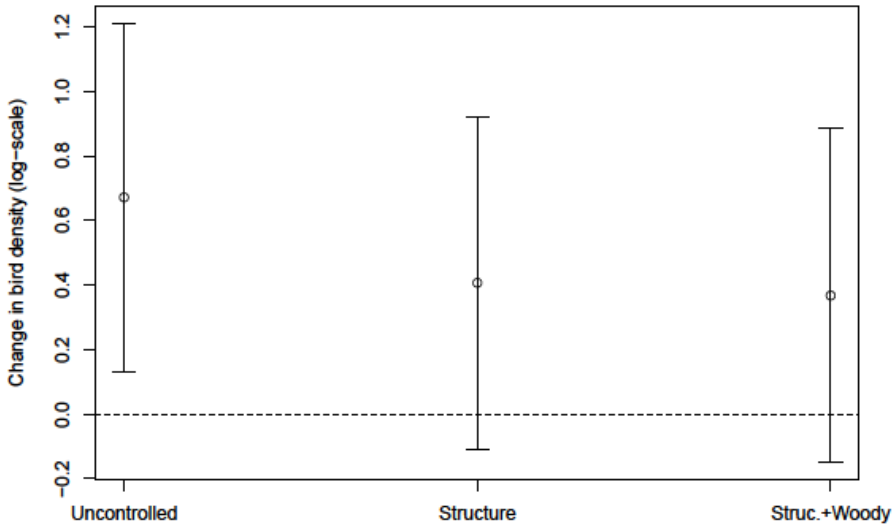

Figure 21. Difference in mean Western Meadowlark abundance between unburned and burned treatments in 2015. Negative values represent lower bird abundance in burned units. Uncontrolled=difference in abundance accounting for detection probability only, Structure=difference in abundance controlling for vegetation structure, Struc+Woody=difference in abundance controlling for difference in vegetation structure and count of woody plants.

CHAPTER IV

CONCLUSION

Remaining habitat for grassland birds is shrinking due to increased demand for conversion of grassland to cropland (Wright and Wimberly 2013), underscoring the importance of managing habitat to benefit the greatest number of bird species. Setting explicit goals for managers such as desired litter depth or vegetation density, requires understanding grassland bird vegetation associations for the region being managed, and not making inferences from studies in other areas. Additionally, understanding how vegetation structure is affected by varying forms of management is key to connecting bird vegetation associations with implementation of on-the-ground management of vegetation. Once preferred levels of vegetation structure are identified for grassland birds, a mosaic of management with those levels of structure can be implemented on the landscape. My study helps to further define the vegetation associations for six grassland bird species, giving explicit targets for vegetation structure that will benefit those species.

This study in the northern tallgrass prairie is particularly important since most inferences about grassland bird responses to vegetation structure come from the southern tallgrass prairie (e.g. Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006) and inferences about grassland bird vegetation associations should not be applied to areas

outside that region. Vegetation associations varied annually for the bird species considered, but birds generally occupied the same vegetation niches. In the county study (Chapter II) there was little influence of woody plants on the density of five of six bird species, with the exception of Clay-colored Sparrow being positively associated with woody plants. When the effect of woody plants was examined at Oakville (Chapter III) more species showed a significant response, with Bobolink, Savannah Sparrow, and Western Meadowlark density all declining in areas with a greater number of woody plants. On Oakville Clay-colored Sparrow was also positively associated with more woody plants. The difference in responses is presumably due to the broader range of woody vegetation present on Oakville versus sites throughout Grand Forks County. The most important determinant of bird abundance at Oakville and county sites was VOR, with percent of grass and bare ground having little influence. As expected, grazed and hayed areas had shorter sparser vegetation with less woody plants and idle areas denser vegetation with higher numbers of woody plants.

The first year of prescribed burning at Oakville had little influence on most measures of vegetation structure, only live vegetation height and litter depth were significantly lower in burned units. Bobolink and Sedge Wren density significantly declined in burned units relative to unburned units, while Western Meadowlark density increased. Interestingly, though not surprisingly, Bobolink and Sedge Wren had VOR replaced by litter depth as the top vegetation structure model the year after burning. The shift in best vegetation structure model suggests that after disturbance some species use amount of litter as a predictor for future vegetation structure, meaning that

birds may associate areas with lower litter with sparse vegetation later in the growing season. Though in our study decrease in litter was not associated with a corresponding decrease in VOR in burned units, so some birds may be present in lower densities when prescribed fire is used alone, when in fact these areas may be suitable based on VOR.

My results suggest that management actions for grassland birds may be most effective if they change VOR. The variety of vegetation associations for the six species I examined reinforces the idea of managing for vegetation heterogeneity on the landscape that has been suggested by others (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Hovick et al. 2015). By having a more diverse mosaic of management types across Grand Forks County, managers could increase the habitat available for the entire range of grassland birds

Literature Cited

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Applied Ecology 41:604–614.

Fuhlendorf, S., W. Harrell, D. Engle, R. Hamilton, C. Davis, and D. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications 25:662–672.

Wright, C., and M. Wimberly. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences 110:4134–4139.